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The study of Nephridia and Genital Ducts since 1895.

By

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With 100 Text-figures.

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INTRODUCTION.

THE title 'Nephridia and Genital Ducts since 1895' has been given to this article because it is an attempt to review from a particular point of view the work that has been done on excretory organs throughout the Metazoa Triploblastica since the publication of my paper 'On the Coelom, Genital ducts, and Nephridia' in vol. 37 of this journal (1895). Like its predecessor the present article, so far as necessary, deals with the coelom as well. It also contains some new original observations.

My main contentions in 1895 were: That much of the uncertainty and disagreement prevalent then in the interpretation of the general morphology of excretory and genital ducts was due to the confusion under the one name nephridium of 'two organs of totally different origin'—(1) the true nephridium, (2) the genital funnel or peritoneal funnel to which the name coelomoduct has since been given (also like 'nephridium' a morphological and not a physiological term).¹ It was pointed out 'that the nephridium is primitively excretory in function, is developed centripetally, as it were, and quite independently of the coelom (indeed, is probably derived from the epiblast), possesses a lumen which is developed as the hollowing out of the nephridial cells, and is generally of an intracellular character, is closed within, and may secondarily acquire an internal opening either into a blood space [this has since been shown not to occur, see p. 140] or into the coelom (true nephridial funnel

¹ When Professor Lankester wrote his interesting 'Introduction' to Part II of the 'Treatise on Zoology' (Lankester, 1900) and adopted my conclusions concerning nephridia, he suggested the name 'coelomoduct' for what I had previously called genital or peritoneal funnel.

as opposed to the peritoneal funnel); and that the second kind of organ, the peritoneal funnel, is primitively the outlet for the genital products, is invariably developed centrifugally as an outgrowth from the coelomic epithelium or wall of the genital follicle, is therefore of undoubtedly mesoblastic origin, and possesses a lumen arising as an extension of the coelom itself' (Goodrich, 1895, p. 479).¹ Further it was shown that these two sets of organs can be followed through the whole Metazoan series from Planaria to Vertebrata; that the nephridium may often be suppressed, at all events in the adult, and excretion carried out by the coelomoduct; and that these two originally separate organs may be combined into a single compound organ of mixed excretory and genital function, since named nephromixium.

At the same time the 'gonocoele theory' of the origin of the coelom, hitherto applied almost entirely to the Platyhelminths and Annelids only, was adopted and extended to all the groups of the Coelomata. It was shown to be consistent throughout with what was known about the structure and development of their excretory and genital ducts.

Many relevant new facts have been discovered since 1895, and it will, I think, be admitted that on the whole they greatly strengthen the foundations of the generalizations briefly outlined above. It is the chief object of this paper to bring together and present this evidence. The literature on the subject is abundant and scattered, and requires very critical analysis if its true value is to be rightly assessed.

¹ It is often stated by authors, whether agreeing with or opposing these conclusions, that according to my theory nephridia must be of ectodermal origin. So far as I am aware I have never made such a rash and dogmatic statement. All that is essential for the theory is that the nephridium should not develop as an outgrowth of the coelomic wall, but have a more superficial origin. The nephridial rudiment may be held to be of ectodermal or of ectomesodermal derivation. There seems to be no hard and fast line between what is called ectodermal and ectomesodermal. To a great extent it is a matter of time of appearance. If the rudiment of a nephridium can be traced back to a superficial cell of an early cleavage stage it is generally held to be ectomesodermal, if it arises at a later stage when the ectoderm is fully differentiated it is generally held to be ectodermal.

We may now, before proceeding farther, define the nomenclature used in this review for the various kinds of paired excretory and genital ducts:

A. Nephridium.

Primitive excretory organ.

a. *Protonephridium*.—Typically with ciliated excretory canal opening to exterior by a nephridiopore; the canal usually has an intracellular lumen, and may branch at its inner end; the canal and its branches end internally and blindly in flame-cells or some specialized form of flame-cell such as the solenocyte (Text-figs. 1, 2, 7).

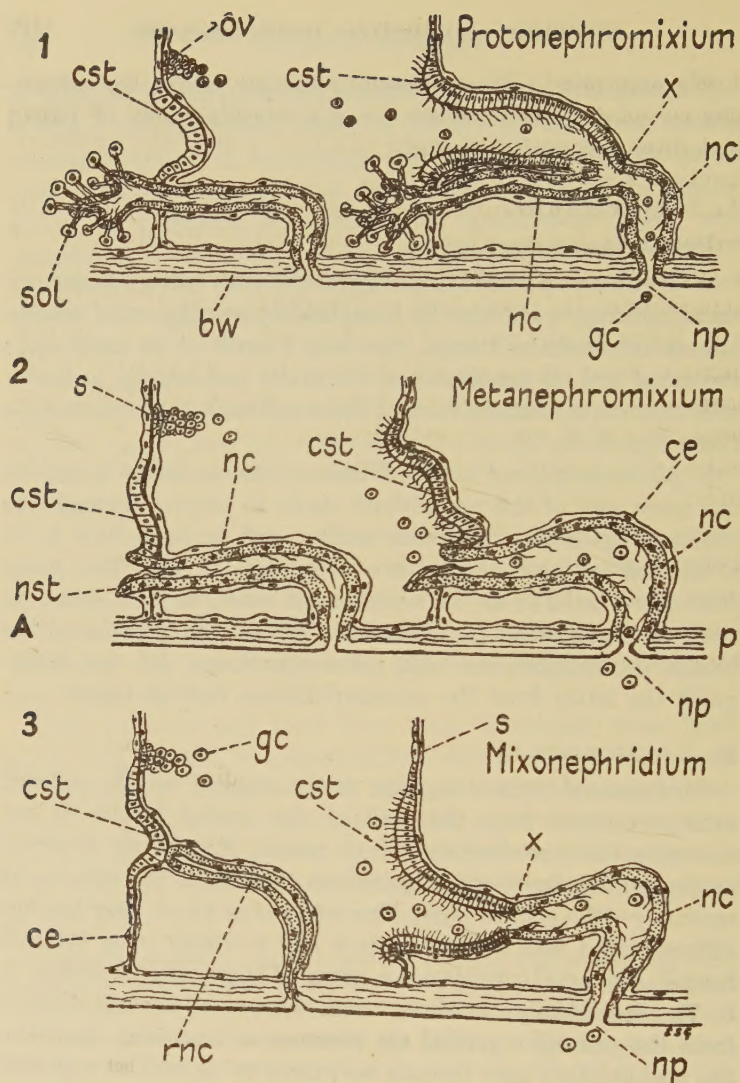
b. *Metanephridium*.—When a coelomic cavity is present the inner end of the nephridium tends to project through the coelomic epithelium into the cavity, and to open into it by a ciliated nephridiostome (Text-figs. 2, 7). The name *metanephridium*, in a restricted sense, is now given to such an organ although Hatschek (1889), who introduced the names *protonephridium* and *metanephridium*, did not distinguish the latter from the *mixonephridium* defined below.

B. Coelomoduct.

This general term is applied to the original tubular ciliated duct developed from the wall of the genital follicle or sac enclosing the reproductive cells or gonad. Primitively it served as the genital duct, and acquired an opening to the exterior at maturity—the genital pore. The *coelomoduct* may become differentiated into a tubular duct and a widely open internal funnel, the *coelomostome* often of large size (Text-figs. 5, 6, 7). Secondly, in those cases where the coelom derived from the primitive genital sac assumes an excretory function, the *coelomoduct* may become an excretory as well as a genital duct, or even become purely excretory losing its primitive genital function.

C. Nephromixium.

Nephridia and coelomoducts usually retain their primitive independence, but sometimes they may become more or less



TEXT-FIGS. 1, 2, 3.

Diagrams showing structure and formation of nephromixia by combination of coelomoduct with nephridium. A, Anterior, young stage before combination. P, Posterior, combination completed. bw, body-wall; ce, coelomic epithelium; cst, coelomoduct; gc, germ-cell; nc, nephridial canal; np, nephridiopore; nst, nephridiostome; ov, ovary; rnc, rudiment of nephridium; s, intersegmental septum; sol, solenocyte; x, point where coelomoduct opens into nephridial canal.

closely associated. Their external pores and even their canals may combine. This combination of nephridium and coelomoduct into one compound organ of mixed genital and excretory function is a nephromixium.

a. *Protonephromixium*.—A nephromixium found in certain Polychaeta, where the coelomoduct (in the form of a coelomostome) is grafted on to the canal of the protonephridium. The pore is both excretory and genital (Text-fig. 1).

b. *Metanephromixium*.—Another form of nephromixium found in those Polychaeta which are provided with metanephridia. The coelomostome is grafted on to the open nephridiostome, and the complex organ so formed may serve either as a genital or an excretory duct or may fulfil both functions (Text-fig. 2).

c. *Mixonephridium*.—When, as in the majority of Polychaeta, the coelomostome is so completely fused to the inner end of the nephridium as to form an apparently simple large-funnelled organ usually capable of performing both excretory and genital functions, it may be called a mixonephridium (Text-fig. 3). Such mixonephridia, until 1895, were not clearly distinguished from metanephridia. This new name is proposed to draw attention to the difference between these two kinds of organ (the metanephridium, and the compound nephromixial organ), often deceptively alike, which it is all-important to understand if a clear conception of the morphological problems discussed in this paper is to be attained.¹ But no hard and fast line can be drawn between a metanephromixium and a mixonephridium. The former name is used when there is clear evidence that the coelomostome has been added to a pre-existing nephridiostome; whereas in the case of mixo-

¹ The failure of so many authors to distinguish between metanephridia and nephromixia (especially mixonephridia), and indeed between even nephridia and coelomoducts, has been and still is the source of much confusion in the literature, particularly in works dealing with physiology and vertebrate embryology. When in doubt, it would be well if writers, who may not wish to commit themselves to any morphological theory of these organs, would make use of such non-committal terms as kidney, excretory, or segmental tubules, and avoid the morphological term nephridium altogether.

nephridia there is often the possibility that the coelomostome may have been grafted on to the blind end of a protonephridium.

It may here be mentioned that both at the nephridiopore and at the coelomoducal pore an invagination of ectoderm may take place, often of considerable size and importance.

The general morphology of the various organs enumerated above is usually very inadequately treated in even the most modern text-books.¹

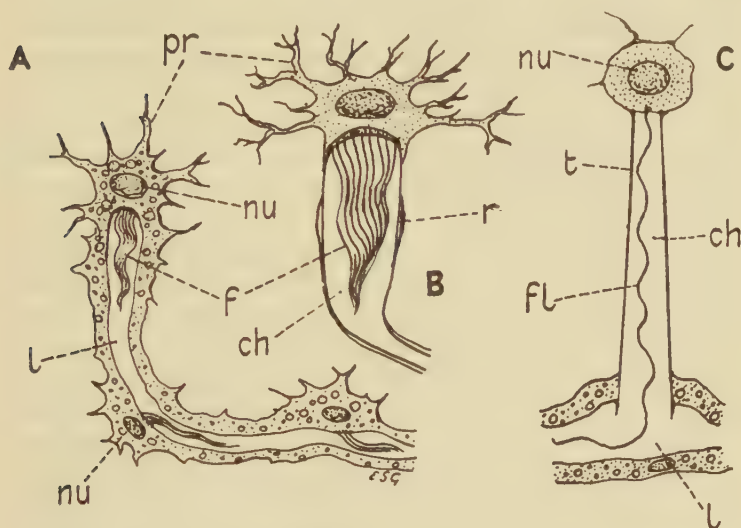
Flame-cells and Solenocytes.

These names are given to various forms of the end-cells which close the inner extremities of protonephridia or their branches. They are the terminal cells of the canal wall. It used to be thought that they were pierced so that the lumen of the canal here communicated with surrounding cavities. The lumen reaches into the end-cell, and there ends blindly. These cells vary considerably in structure, from 'flame-cell' to 'solenocyte' (Goodrich, 1898). A typical flame-cell, such as Lang described in Polycladida (1884), has irregular cytoplasmic processes extending to neighbouring cells of the parenchyma, and a large central nucleus in the cell-body (Text-fig. 4). That part of the cell which encloses the blind end of the lumen is thinned out to form a chamber in which undulates a flame-like bunch of cilia attached below the nucleus. Usually the cell itself seems to contain few if any excretory granules, and the

¹ An unfortunate example is 'The Invertebrata' (Cambridge, 1932), where the chapter on Annelida contains not only pardonable misinterpretations but plain errors of fact. Some of them were corrected in the second edition (1935), but others were added. On p. 275 it is stated that the open nephridium may take on the function of the coelomoduct. On p. 276, Fig. 1 E is wrongly attributed to the Capitellidae, and it is stated that in this Capitellid 'the funnel of the coelomoduct has completely fused round the opening of the nephridium'! On p. 277 it is stated that 'In the majority of polychaetes, however, the coelomoduct has disappeared altogether'! And that *Glycera* and *Nephtys* have open nephridia! The fact is that both have closed protonephridia, and that *Nephtys* is the polychaete in which solenocytes were first discovered! On the same page the legend below the figure of the nephridium of *Glossiphonia* describes it as showing the 'mesodermal part with ciliated nephrostome', thus implying that the whole organ is a nephromixium!

chief function of the 'flame' is to drive the fluid passing by osmosis through the thin wall of the chamber down the canal towards the nephridiopore.

In adaptation to this function, the wall of the chamber tends



TEXT-FIG. 4.

A, Inner end of branch of nephridial canal of a Polyclad Turbellarian with typical flame-cell at extremity (from Lang's figures). B, Flame-cell of a Cestode. C, Typical solenocyte of Polychaete. All diagrammatic. *ch*, terminal chamber of protonephridial lumen; *f*, flame of cilia; *fl*, flagellum; *l*, lumen of protonephridial canal; *nu*, nucleus; *pr*, cytoplasmic processes; *r*, strengthening ring; *t*, tube.

to become thinner and more membrane-like, until in the typical solenocyte it forms a long narrow, more or less cylindrical, tube bearing the cell-body at its free end. At the same time the bunch of cilia is reduced to a single long flagellum, which vibrates vigorously and reaches far into the lumen of the canal (Text-fig. 4, c).

Other specializations may occur, such as the shifting of the nucleus and cell-body away from the apex of the chamber or tube, and the development of several flame-holding chambers or

several flagellated tubes to each nucleus. These will be described in the groups in which they occur.

It is important to realize that protonephridia with such end-cells are now known to occur in the adult, not only of *Platyhelminia* generally, but also of *Rotifera*, *Nemertina*, *Acanthocephala*, *Priapulida*, *Endoprocta*, *Gastrotricha*, *Kinorhyncha*, and *Cephalochorda*, and in some *Archiannelida* and *Polychaeta*. Also in the larval stage of *Polychaeta*, *Archiannelida*, *Echiuroidea*, *Mollusca*, *Phoronida*, and *Cephalochorda*. These organs are in fact very widely distributed, and may be inferred to have been present in the common ancestor of all the *Metazoa Triploblastica*.

Of all the general works which have appeared on nephridia and related subjects since 1895 that of Fage (1906) is the most important. In addition to a discussion on the general morphology and physiology of nephridia and coelomoducts, it contains a series of valuable observations on these organs in the *Polychaeta* confirming and extending my own descriptions and conclusions. The work of Fage will be frequently referred to below.

Several general discussions have been published, notably by E. Meyer (1901), Lang (1903), Montgomery (1908),¹ and Meisenheimer (1909). Those of Willem (1910), de Beauchamp (1911),

¹ Montgomery's review 'On the Morphology of the Excretory Organs of Metazoa' contains a useful list of the literature with brief accounts of the work done up to 1908; but the author's own conclusions are complicated and often difficult to understand. His grouping of such excretory organs as those of *Turbellaria* and the Malpighian tubes of *Insecta* as homologous protonephridia seems not to be supported by sound evidence. His division of various excretory organs (including nephromixia) into those without and those with an alleged third retroperitoneal mesentoblastic element between coelomostome and nephridial canal and pore is to me quite unintelligible.

Meisenheimer (1909) deals with 'Protonephridien und typische Segmentalorgane'; he also reviews the literature critically, describing in some detail the protonephridia found in the various groups from *Platyhelminia* to *Cephalochorda* and their development, and the protonephridial larval organs including his own important work on *Mollusca*. Notwithstanding certain differences in the accounts of various authors, he comes to the conclusion that all these organs are homologous and of ectodermal origin. Coming to the open excretory organs of *Annelida* and nephromixia he

and Burian (1913) should also be mentioned, and Saarvas (1933) on the coelom (with most of her morphological conclusions I am unable to agree).

The interpretation of the morphology of nephridia and coelomoducts is intimately connected with the theory of the origin of the coelom. This problem was briefly dealt with in my article of 1895, where it was pointed out how well the 'Gonocoele Theory' fitted in with what was then known of the structure and development of excretory and genital ducts in the various groups of the Metazoa Triploblastica. If this was true in 1895 it is still truer to-day. The Gonocoele theory was founded by Hatschek (1878) and E. Meyer (1890) chiefly on a comparison of the Turbellaria with the Annelida, and in particular with the Polychaeta. Later it was extended in some detail by me to the other groups of Coelomata (Goodrich, 1895), taking into consideration more especially the relations to the coelom of nephridia and coelomoducts. Many new discoveries have strengthened the foundations of the theory since then.

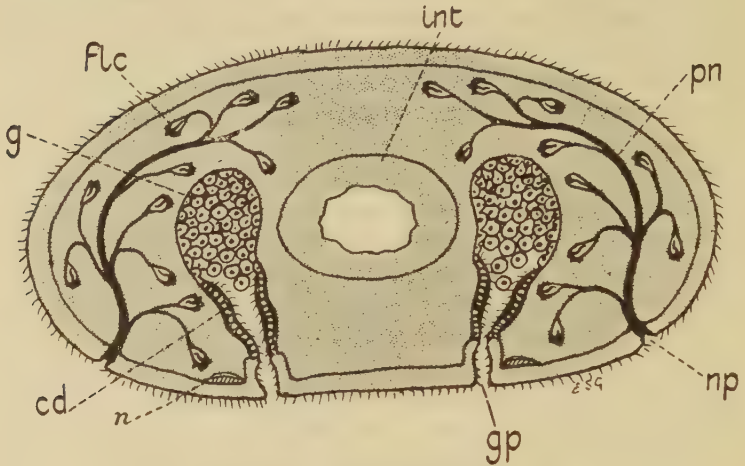
Two important works on the Gonocoele Theory have appeared more recently: one by E. Meyer (1901), and the other by Lang (1903). Lankester's (1900) short but masterly essay on the coelom and related subjects should also be mentioned here.

According to this theory paired coelomic sacs, developed from embryonic somites, have been derived phylogenetically from the paired gonadial sacs or genital follicles occurring in the lower Triploblastica (Platyhelminia, Rotifera, Nemertina, &c.). accepts my general interpretation; but makes the suggestion, which I believe to be erroneous (see p. 298), that in the Hirudinea the funnel attached to the nephridium is a coelomostome.

Willem (1910) accepts my views on the morphology of nephridia and coelomoducts, and adds some interesting observations especially on the physiology of these organs in various groups which will be mentioned later.

Burian, in vol. 2 of Winterstein's Handbuch (1913), deals with nephridia, nephromixia, and ciliophagocytal organs in Annelida particularly from the physiological point of view. It may be mentioned that he reproduces on pp. 315, 316, 317 several of my figures copied by Meisenheimer, and describes them in the legends as 'Nach Meisenheimer'! Several of these figures reappear in Jordan's 'Allgemeine vergl. Physiologie' (1929), also 'nach Meisenheimer'. Jordan attributes some of my work on the nephridia of *Amphioxus* to Willem!

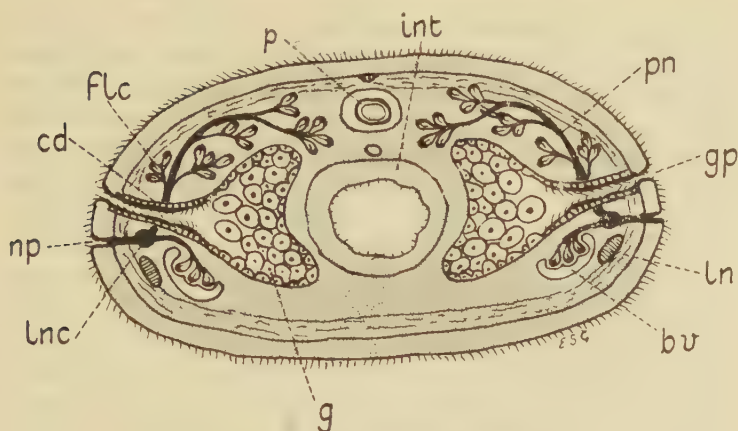
The theory may be briefly stated as follows: The germ-cells arise from the wall of these follicles just as in the higher forms they arise from the wall of the coelom (Text-fig. 5). Although in the earliest phylogenetic stage common to all Triploblastica the genital follicle may have been represented by a mere accumulation of germ-cells between ectoderm and endoderm,



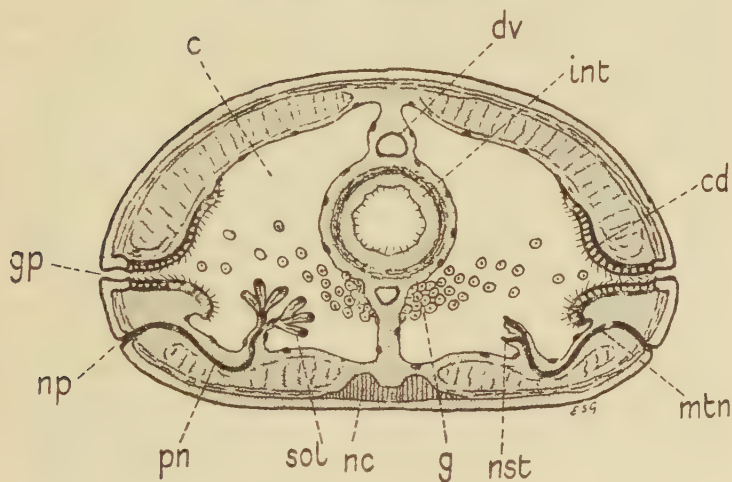
TEXT-FIG 5. Platyhelminth stage.

Diagrams showing homologies of nephridia and coelomoducts, and origin of coelom, in transverse sections of Text-fig. 5, the Platyhelminth stage; Text-fig. 6, the Nemertine stage; and Text-fig. 7, the Annelid stage. *bv*, lateral blood-vessel; *c*, coelom; *cd*, coelomoduct; *dv*, dorsal longitudinal blood-vessel; *flc*, flame-cell; *g*, gonad; *gp*, genital pore; *int*, intestine; *ln*, lateral nerve; *lnc*, longitudinal nephridial canal; *mtn*, metanephridium; *n*, ventral longitudinal nerve; *nc*, ventral longitudinal nerve; *np*, nephridiopore; *nst*, nephridiostome; *p*, proboscis; *pn*, protonephridium; *sol*, solenocyte.

it soon tended to become differentiated into more central gonadal cells and more peripheral covering cells; the former being derived from that proliferating portion of the wall destined to form the true gonad, and the latter being that portion of the wall destined to form the lining epithelium and the outgrowing coelomoduct. So long as gonad and its covering epithelium



TEXT-FIG. 6. Nemertine stage.



TEXT-FIG. 7. Annelid stage.

grew at about the same rate a solid organ would result (so-called testis and ovary of *Platyhelminia*); but if the epithelium grew faster than the gonad itself, and if the growth and ripening of the gonad were delayed, a cavity would appear. This cavity (the coelom), containing fluid, would become filled with developing germ-cells from the proliferating gonad towards the

time of sexual maturity. As the coelom enlarged it would tend to acquire new properties and functions. Essentially it is a prematurely developed gonadial cavity, tending to appear early and persist throughout life as the 'body cavity'. Nutritive substances could be carried in the contained fluid, waste materials could gather in it, and phagocytal cells drop into it. The nephridia would naturally become related to the coelom and tend to penetrate its wall. The coelom would also acquire mechanical functions connected with motion, enabling the free movements of the heart and alimentary canal to take place, and the turgidity of soft-bodied animals to be kept up. Thus, without inventing phantastic ancestors, the Gonocoele Theory helps us to visualize how step by step the coelom arose, each phylogenetic stage functionally efficient and paralleled in some animal living at the present day (Text-figs. 5, 6, 7).

The development of metameric segmentation in elongated Coelomata is probably an adaptation to rapid movement, but is also related to that tendency towards the repetition of organs in regular sequence already so conspicuous in *Platyhelminia* and *Nemertina*. This tendency might, when associated with teloblastic growth, lead to the formation of a posterior zone of growth and of successive metameres intervening between prostomium and pygidium in regular order from before backwards. Each such metamere would include a pair of coelomic sacs and corresponding coelomoducts (Text-figs. 13, 19). A division of labour between the segments generally results in the restriction of the reproductive function to certain segments in the middle region of the trunk where alone gonads and ducts are fully developed, while these organs, in the anterior, and sometimes in the posterior segments as well, fail to develop and these segments become sterile.¹

¹ Snodgrass (1938) in his discussion on the 'Evolution of Annelida, Onychophora, and Arthropoda' seems to attach too much importance to Iwanoff's (1928) distinction between primary and secondary somites, a distinction of very doubtful value which, if it occurs at all, only does so apparently in a few Polychaeta. Snodgrass in this paper makes several erroneous statements such as: that metanephridia never occur in the 'primary' segments; that it is 'now established that the metanephridia of the annelids in general are structures of the nature of coelomoducts',

As is so clearly seen for instance in the earthworm, this restriction of the gonads and their ducts need not directly affect the distribution of the true nephridia. The disappearance of these organs is related to other factors such as the loss of the excretory function in the buccal and pharyngeal regions; as growth proceeds anterior nephridia may become progressively replaced by others in segments farther back. But when the coelomoduct secondarily becomes excretory (either as a whole, or in the form of the coelomostome of a nephromixium) it may develop and even persist in quite anterior segments, as in some Annelida, many Arthropoda, and certain other forms.

Of all the objections which have been urged against the Gonocoele Theory the only one deserving serious consideration relates to the modern views about the precocious segregation of the germ-cells. For it is now held that in a large number of Coelomata the primary germ-cells do not originate from the lining epithelium of the genital follicle (coelomic sac), but are developed from the endoderm or in early cleavage stages as a distinct rudiment separate from that of the coelomesoblast. The primary germ-cells would, then, only secondarily become included in the coelomic epithelium. This early and separate segregation does not appear to take place among the lowest forms, such as Platyhelminia, Nemertina, and Annelida, but rather in such higher more specialized groups as the Arthropoda and Vertebrata, and other groups like the Phoronida and Nematoda with specialized early development. Whether the p. 49; and, most astonishing of all, that in the solenocyte of the adult annelid the flagellum is 'said to be nonmotile', p. 46. As a matter of fact it is the active flickering of this flagellum which usually first attracts the attention of the observer!

He also concludes that the Gonocoele Theory 'entirely breaks down in view of the fact that the primary larval somites of the annelids do not contain germ-cells', p. 17. In answer to this strange argument it may be pointed out that, whether the two primary mesoblastic teloblasts derived from cell 4*d* contain the substance of the future germ-cells or not, it is certain that the rudiment of these germ-cells is somewhere in the embryo even before it becomes metamerically segmented. Exactly how this rudiment becomes distributed in an active form to the various segments in no way affects the validity of the Gonocoele Theory. It is, indeed, part of the Theory that some segments may remain sterile forming coelom only.

early segregation of germ-cell material is primitive or not still remains to be determined. Whatever the final verdict may be, it should be realized that it will not be fatal to the Gonocoel Theory. For, whatever may be the origin of the primary germ-cells in embryology, it is clear that they must always finally take up a position in the wall of the gonadial sac where they can proliferate and drop their products into the coelomic cavity. That is all that is essential for the Theory.

It may finally be pointed out now that, in addition to explaining the general relations of nephridia and coelomoducts, the Theory also helps us to understand the general morphological relations of the connective tissues, the musculature, and the haemal system, as well as the formation of mesenteries and transverse septa in segmented animals. Further it offers an explanation of the paired character of the somites and coelom, and the absence of coelom from the prostomial and pygidial regions.

We need not here discuss the various embryological questions related to the origin of the coelom, such as the nature of the germ-layers; but it may be pointed out that the Gonocoel Theory is in harmony with modern views about the complex make-up of the 'mesoderm', and the distinction between ectomesoderm (ectomesoblast, mesenchyme, larval mesoblast, &c.) and coelomesoderm from which arise the gonads and their ducts, certain muscles, and in segmented animals the mesodermal somites and coelomoducts, but not the nephridia.¹

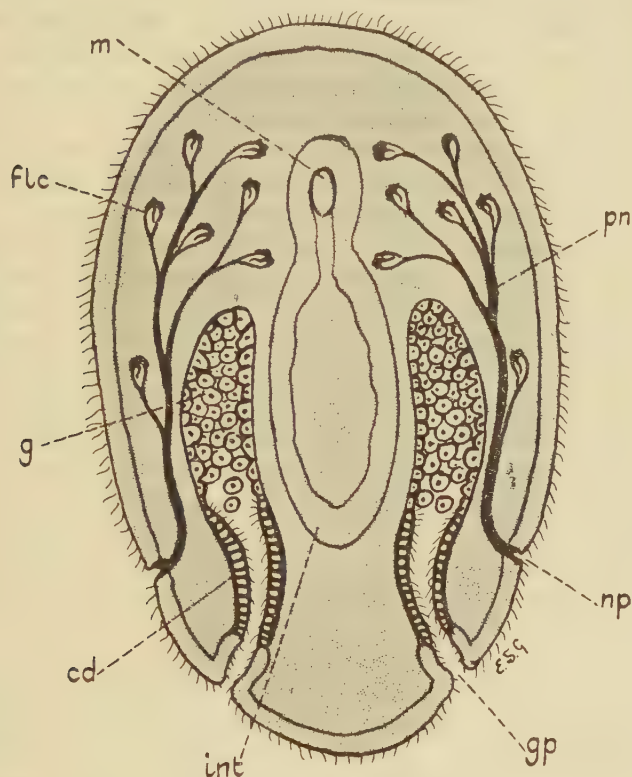
Phylum Platyhelminia.

Already in 1895 the excretory system of the Platyhelminia was fairly well known. It consists of a pair of protonephridia of typical structure. Each external pore leads to a main longitudinal canal which gives off many delicate branches ending in flame-cells scattered widely in the parenchyma (Text-fig. 8). But this simple type is subject to great variation in detail in the different groups.

In the Turbellaria Rhabdocoelida the pores may shift

¹ These problems the reader will find discussed in detail in the works of E. Meyer (1901) and Lang (1903) already mentioned, who subject the Enterocoel and Nephrocoel theories to well-deserved and severe criticism.

from a posterior to an anterior position, may be carried into the peripharyngeal sac (Mesostoma), or the genital atrium (Typhloplanidae), or may join to a median posterior opening



TEXT-FIG. 8.

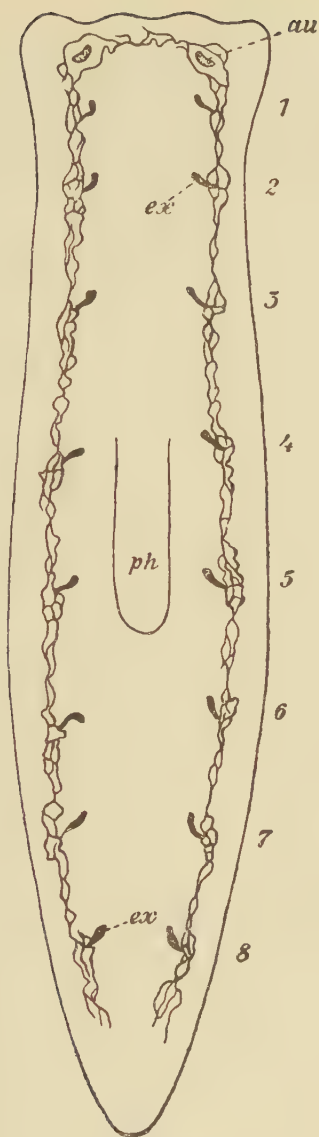
Plan of a primitive Platyhelminth. *flc*, flame-cell; *g*, gonad; *gp*, genital pore; *int*, intestine; *m*, mouth; *np*, nephridiopore; *pn*, protonephridium. Dorsal view.

(Plagiostomum). In *Stenostoma* the main canals join to a median trunk. Transverse connexions exist between the two nephridia in *Prorhynchus* (von Graff, 1907), also in the Alloiocoelid *Bothrioplana*, where two median pores occur (Vejdovsky, 1895). The Tricladida have a network

of anastomosing canals extending in front from right to left side (Text-fig. 9), and opening by a series of pores on each side regularly arranged in *Dendrocoelum* (Ijima, 1884; Wilhelmi, 1906; Micoletzky, 1907), and *Procerodes* (Lang, 1881; Böhmig, 1906). Lang has suggested that the numerous and segmentally disposed nephridia of the higher worms have arisen by the subdivision of such a longitudinal system into separate organs corresponding to the pores (Lang, 1881, 1903). Sometimes, as in *Polycystis* (Bresslau, 1904), the external pore leads into a muscular contractile bladder, doubtless an invagination of the body-wall.

The *Temnocephala* have paired protonephridia of peculiar structure (Haswell, 1893, 1909). The two main longitudinal canals, generally joined together by anterior and posterior anastomosing canals, lead to a more superficial set of arborescent finer branches ending in flame-cells. Some of the branches ramify in the cytoplasm of large excretory cells. Each main canal opens at a lateral, or usually dorsal pore, by a contractile bladder covered by two cells. The outer cell receives a special branch canal which ramifies in its cytoplasm, the very numerous terminal twigs being provided with small flames. The whole system of canals has an intracellular lumen and is excavated in relatively few cells with large nuclei, as shown by its development (Haswell, 1909).

The *Trematoda* show a similar variety of structure. Relatively simple in the *Heterocotylea* (*Monogenea*) with paired anterior pores, it may become more specialized in the *Malacotylea* (*Digenea*). Here the main canals join to a pore usually posterior as in *Distomum*, and may form an anastomosing network with from four to eight longitudinal trunks (*Octangium*, Looss, 1902). Moreover, the posterior contractile median bladder formed by the invagination of the epidermis may be highly specialized with sphincters, diverticula, and a cuticular lining bearing spinous processes (Brown, 1899; Looss, 1902). A similar pair of protonephridia occurs in the larval stages. The miracidium of *Distomum hepaticum* has on each side a single flame-cell with a slender canal opening by a pore between the large ectodermal cells (Coe, 1896; Ortmann,



TEXT-FIG. 9.

Dendrocoelum lacteum, protonephridial network of canals and pores, flame-cells not shown (after Wilhelmi, 1906, from Meisenheimer, 1909). *ex*, nephridiopores; *ph*, pharynx; *au*, eyes.

1908). That of *Heronimus chelydrae* may have a second flame-cell (Lynch, 1933) and in *Schistosomum haematobium* the branching canal leads to three flame-cells (Reisinger, 1923). Protonephridia with a varying number of flame-cells have also been described in the sporocyst, redia, and cercaria stages.¹

The protonephridia are much developed and specialized in the Cestoidea. There is generally a more superficial network of canals receiving fine tributaries from numerous flame-cells and a system of usually four main longitudinal canals, with more or less regular transverse connexions in the adult (Fraipont, 1880; Pintner, 1880, 1906; Bugge, 1902).

The Cestodaria (Cestoidea monozoa) have an extensive network, without longitudinal canals and opening by paired lateral pores in *Gyrocotyle* (Spencer, 1889), but by a median posterior bladder and pore in *Amphilina* (Hein, 1904).

In the young Cestoidea mesozoa the system consists on each side of a dorsal longitudinal canal passing in the scolex into a ventral canal. The two ventral canals open by a median contractile bladder and posterior pore (Pintner). As the proglottids drop off the canals come to open directly to the exterior, and further numerous small openings, foramina secundaria, may be formed in addition. In the proscotex stage the combined protonephridia open by a median pore in front of the deciduous 'tail'.

From the above brief description it may be concluded that, in spite of endless modifications of detail, the excretory organs may be derived in all these flatworms from a pair of protonephridia similar to those of the more primitive Turbellaria. The system spreads throughout the parenchyma to carry out its functions, the chief part of the flame-cells being apparently to remove water from the tissues, and so regulate their water content as well as to flush the canals. The waste substances are collected as droplets and granules in the walls of the canals

¹ At first the cercaria has two lateral nephridiopores which come to open on the 'tail'. Later a median ventral depression of the epidermis appears farther forward to which the two canals become connected; so that, when the 'tail' drops off, the protonephridia still open to the exterior.

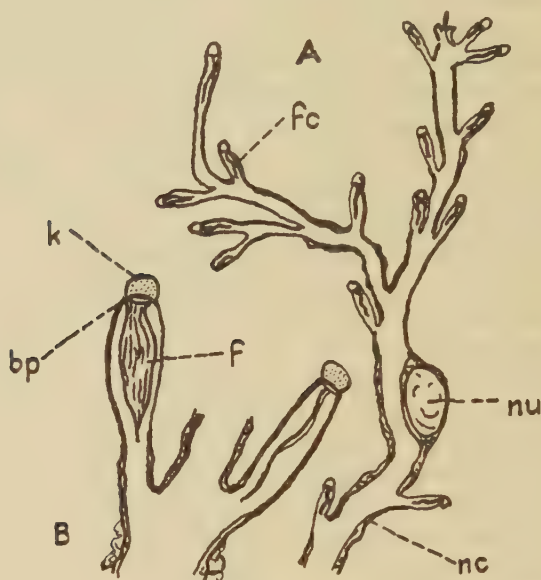
to be shed in their lumen. Groups of athrocytic cells, the paranephrocytes, which accumulate waste material, and are derived from the parenchyma are sometimes found associated with the nephridial canals in the Rhabdocoelida (Reisinger, 1922; Westblad, 1926).

Concerning the finer structure of the protonephridial canals it may be mentioned that the lumen of the smaller branches is intracellular, but in the larger canals it becomes intercellular. They may be more or less ciliated throughout, or the cilia confined to regions, sometimes disposed in 'flames', as in *Mesostoma* (Luther, 1904), and *Cercariaceum* (Bugge, 1902), or in longitudinal bands, as in *Gyrocotyle* (Spencer, 1889). Cell boundaries are usually not visible; in *Cestoidea mesozoa*, where cilia are absent, a cuticular layer separates the granular cytoplasm from the lumen (Bugge, 1902).

The finer structure of the flame-cells varies also considerably. What may probably be considered as the most primitive type is seen in *Polycladida* (Text-fig. 4A) where excretory granules occur in the cell-body (Lang, 1884); *Rhabdocoelida* (Luther, 1904), *Tricladida* (Wilhelmi, 1906; Willem, 1910), and *Trematoda* (Bugge, 1902; Rudin, 1914) generally have more specialized flame-cells. The terminal branch or 'capillary' has a slightly expanded lumen at its apex, which is closed by the cell-body containing the nucleus. Irregular processes may spread from the cell into the surrounding parenchyma. Attached to the cell near the nucleus is a flattened 'flame' of cilia vibrating in the lumen. Willem found no processes in *Distomum clavigerum*, and Reisinger (1923a) no nucleus at the base of the flame in *Mesostoma* (Text-fig. 10) or the miracidium of *Schistosomum*; in *Cestoidea* and many *Trematoda*, however, both radiating processes and nucleus seem to be undoubtedly present. The cilia of the flame are provided with basal granules, and are attached to a plate of dense deeply staining substance. Moreover, especially in *Trematodes* and *Cestodes*, the wall of the terminal chamber becomes thin, membranous, or cuticular, often with a strengthening circular thickening (Text-fig. 4B), and a space filled with liquid may surround it (Bugge, Reisinger, Ortmann, 1908).

These specializations no doubt facilitate osmosis, and the flame-cell comes to resemble the typical solenocyte of higher forms.

The observations of Bugge (1902), in the Trematode *Dicrocoelium*, of flame-cells provided with several flames, and of Hein (1904), in *Amphilina*, of large flame-cells with branch-



TEXT-FIG. 10.

Mesostoma ehrenbergii. A, Terminal branch of protonephridium (*nc*) with several 'flame-cells' (*fc*) but only one nucleus (*nu*). B, Two end-organs on larger scale. *bp*, basal plate; *f*, flame of cilia; *k*, endknob (Reisinger, 1923).

ing central chamber and many flames are of interest, for in the Archiannelida one nucleus may also 'control' several solenocyte tubes and flagella (see p. 215). Important points to determine are whether the flame-cells and the excretory cells of the canals are derived from a common rudiment (*Anlage*), and are of ectodermal origin. This is the conclusion of most modern authors; indeed, the only one who believes that the flame-cells are separately developed from mesodermal parenchyma cells is Young (1908). But his observations on *Cysticercus pisi-*

forms are unconvincing, and cannot be accepted in view of their extreme unlikelihood and the contrary observations of others on *Platyhelminia* and other forms.

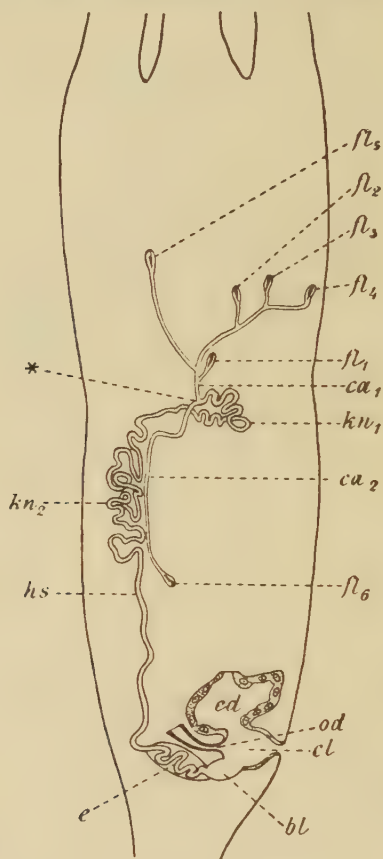
Unfortunately little progress has been made in the difficult task of tracing the embryonic development of the protonephridia in *Platyhelminia* since Lang (1884) first described their origin from paired ingrowths of ectodermal cells in the Polyclad *Discocoelis*. Bresslau (1904) derived them from similar ingrowths of ectoderm on either side of the mouth in *Mesostomum*, where they grow into strings of cells which become hollowed out by an intracellular lumen. But the difficulty of tracing their very first origin has not yet been overcome completely. Bugge (1902) and Rossbach (1906) have described the development of similar strings of cells which give rise to both canal and flame-cells in *Trematoda*, and Goldschmidt (1905) traced the origin of flame-cell and canal more in detail from ectodermal cells in the miracidium of *Zoogonus minus*.

That the flame-cells are derived in later stages from the wall of the protonephridial canal has been well shown by Bugge (1902) in Trematodes and Cestodes. In Cestodes the body of the nephridial cell containing the nucleus may be drawn away some distance, remaining, however, in continuity with the canal wall. Such a cell may divide twice, giving rise to a group of four nucleated cells, one of which remains to form the hollow connecting 'capillary', while the other three grow into flame-cells whose cavities communicate with it.

Thus, though more evidence is much needed, it can hardly be doubted that the whole protonephridium in *Platyhelminia* generally is derived from one and the same rudiment, and, further, that this rudiment is a cell of superficial and probably of ectomesodermal or ectodermal origin.

Little detailed work on the origin of the genital ducts seems to have been done of late. The modern *Platyhelminths*, although so primitive in their general plan of organization (Text-figs. 5 and 8) are highly specialized in the structure of their gonads and coelomoducts. They are almost invariably hermaphrodite and often the gonadial sacs become not only subdivided into 'testes' and 'ovaries', but may branch with correspondingly

branching ducts. The ducts usually join an unpaired atrium of ectodermal origin, and provided with a complex copulatory apparatus. Nevertheless, the genital ducts appear to develop like coelomoducts as evaginations of the gonadal sacs (Lang, in Triclad, 1882, and Polyclads, 1884; Kenk, 1924). The



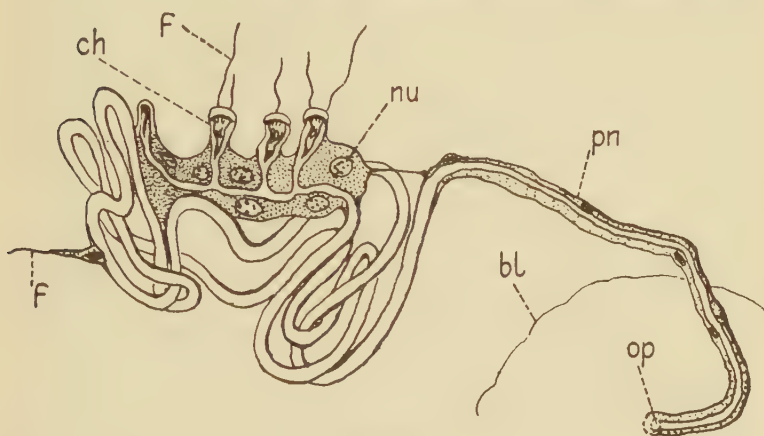
TEXT-FIG. 11.

Stephanoceros fimbriatus, side view of protonephridium and cloaca (after Montgomery, 1903, from Meisenheimer). *bl*, contractile bladder; *ca*, capillary canal; *cl*, cloaca; *e*, median canal; *ed*, end-gut; *fl*, flame-cell; *hs*, main canal; *kn*, coiled region; *od*, oviduct.

sometimes fragmentary condition of the ducts of certain Acoela must be considered as due to degeneration.

Phylum Rotifera.

It has long been known that the Rotifera (Rotatoria) are provided with a pair of protonephridia. Since 1895 certain interesting details have been made known by Montgomery (1903), Hlava (1904, 1905), Shephard (1899), Willem (1910)



TEXT-FIG. 12.

Protonephridium of *Asplanchna priodonta* (from Willem, 1910). *bl*, bladder; *ch*, chamber with flame; *f*, fixing filament; *nu*, nucleus; *op*, opening of canal into bladder; *pn*, protonephridial canal.

Martini (1912), Nachtwey (1925), and others. The two protonephridia join posteriorly to open by a median pore and contractile bladder into the cloaca together with the gut and genital duct (Text-fig. 11). The flame-cells, which project into the extensive pseudocoelic spaces, attached to neighbouring structures by delicate filaments, vary considerably in structure. Rarely they are of typical form with apical cell-body and nucleus (Gast, 1900, in *Apsilus*; Hlava, 1905, in *Megalotrocha*); but usually the flame springs from an apical end-plate, the nucleus being in the wall of the canal (Text-fig. 12). The canal is generally much convoluted, and has a special thick-walled

glandular region; flagella or flames may be present in its intracellular lumen. Nachtwey (1925) in *Asplanchna* has traced the protonephridia of the early embryo to right and left small groups of cells, which appear to be of ectodermal or ectomesodermal origin. At a later stage the rudiment consists of three large and four small cells from which develop the canal and the four flame-cells respectively of the adult syncytium of this species.

The genital organs are built on essentially the same plan as that shown in Text-fig. 9 as paired gonadial sacs provided with coelomoducts. But in both sexes they become considerably specialized. The ducts join to open by a single pore into the cloaca, and in the female the sac and duct of one side is usually lost.

Phyla Gastrotricha and Kinorhyncha.

A good general account of the structure of these small worms of doubtful affinity has recently been given by Remane (1936).

The Gastrotricha have no distinct body-cavity, their organs are closely packed and mostly enclosed in membranes. Most of them have a pair of protonephridia first noticed by Bütschli and well described since by Zelinka (1889). The coiled canal with intracellular lumen is differentiated into a posterior glandular region opening by a ventral pore, and an anterior capillary region ending blindly in front in a single flame-cell with one flagellum but no apical nucleus.

The Gastrotricha are usually hermaphrodite with male and female originally paired genital sacs and ducts. The male ducts open together ventrally by a median pore. The ovisacs unite to a median oviduct which opens to the exterior or together with the anus.

The Echinodera (Kinorhyncha) also have a pair of protonephridia, discovered by Reinhard (1887) and well described by Zelinka (1908). Each consists of a short syncytial canal with several nuclei in its wall. At the blind anterior end of the lumen is one long flagellum and sometimes a short one as well. Along the course of the lumen which opens by a posterior lateral pore, there are other flagella. Schepotieff's statement that there

are three pairs of such protonephridia in *Echinoderes* (1907) has not been confirmed.

The gonads shed their products into paired sacs, which have separate posterior openings. The extensive body-cavity has no regular epithelial lining and appears to be of pseudocoelic nature.

In both these groups the gonadial sacs and genital ducts no doubt represent the coelomic sacs and their coelomoducts, and may be derived from the general plan shown in Text-fig. 9.

Phylum Nematoda.

These very specialized elongated unsegmented worms, often internal parasites, have no general coelomic body-cavity, and no vascular system. Paired ovarian tubes in the female and median testicular tubes in the males and the genital ducts into which they are prolonged probably represent the coelom and coelomoducts. The oviducts join to a ventral median vaginal pore far forward. The spermoduct usually opens posteriorly into a cloaca with a median pore armed with a spicula.

Paired longitudinal canals in the lateral thickenings of the body-wall are considered to be the excretory organs. The system has neither cilia nor internal opening, and consists of canals which join across in a bridge of tissue to a median duct opening far forward by a median ventral pore. The whole organ is formed of only two cells excavated by an intracellular lumen, more or less subdivided anteriorly, and lined with a cuticula. One cell, said to be derived from the ectoderm, includes the median duct. The remainder, including the lateral canals (one only may be present) and transverse connexion, is formed of a single giant cell with its nucleus on the left side. The morphological significance of this organ is obscure (A. Schneider, 1866; Hamann, 1895; Jagerskiöld, 1894; Goldschmidt, 1906).

Phylum Nematomorpha.

Highly specialized elongated worms, aquatic or parasitic in habit, and generally considered to be allied to the Nematoda. They appear to have no coelomic body-cavity, no vascular system, and no excretory organs. The coelom is probably

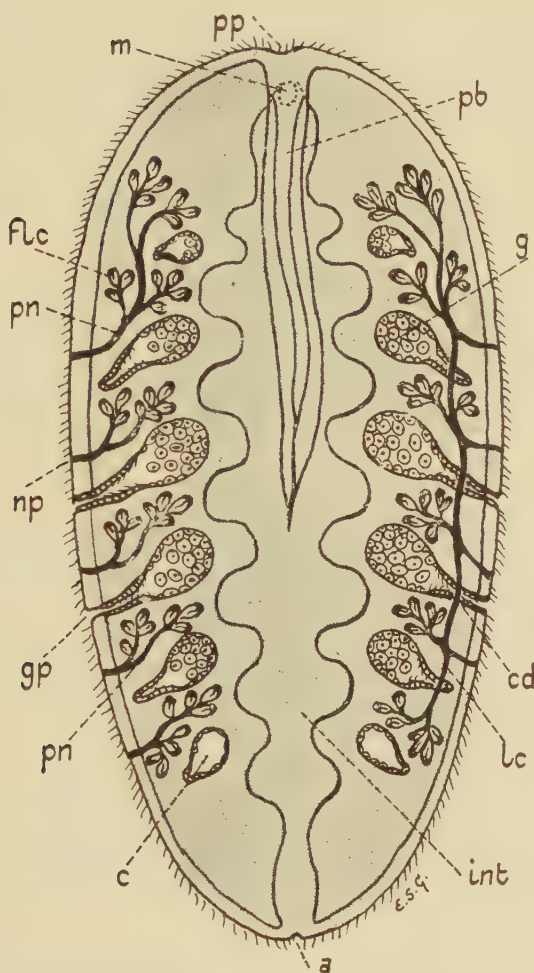
represented by the paired gonadial tubes prolonged posteriorly into two genital ducts which open together with the anus into a cloaca. These ducts may be considered as coelomoducts. The occurrence in the female of a regular series of lateral ovarian pouches from each of the gonadial tubes in Gordiidae led Vejdovsky (1874, 1886) to suggest that they are descended from segmented Annelida; but this view has not been generally accepted (Villot, 1874, 1881; Montgomery, 1903; Rauther, 1905).

Phylum Nemertina.

Although nothing of great morphological importance seems to have been added to our knowledge of the nephridia of the Nemertina since the work of Bürger (1890, 1892, 1895), many interesting details have since been brought to light. Bürger showed that the nephridia are of the protonephridial type (Text-figs. 6 and 13). They are paired more or less branching canals opening to the exterior by one or more efferent ducts, and their inner ends branch into delicate twigs leading to terminal flame-cells. The latter are usually closely related to the blood-vascular channels, but do not open into them.¹

These protonephridia vary much in form and in number. A good general and historical account of them will be found in the works of Bürger (1895, 1897-1907). Usually there is a single pair situated far forward near the brain. Each may consist (as in *Cerebratulus*) of a system of branched relatively thick-walled canals leading to an efferent duct, which pierces the epidermis at the pore. These canals and duct have an intercellular lumen and are more or less completely ciliated internally.

¹ Before Bürger showed that the nephridial tubules ended in flame-cells, it was held by several observers that they opened into the blood-vessels (Ondemans, 1885). This view is now generally discredited, but has recently been revived by Nawitzi (1931) and Friedrich (1935), who state that in the Palaeonemertines *Procarinina* and *Carinina* a terminal thick-walled part of the canal ('Nephridialdrüse') not only projects into the lateral blood-vessel, but that its lumen communicates by narrow channels with the blood-space. The figures given, however, afford no convincing evidence of such communication.



TEXT-FIG. 13.

Diagram of a Nemertine, showing paired series of genital sacs, and adult series of separate protonephridia, *pn*, on left side. On right side is shown the young stage with single protonephridium and longitudinal canal, *lc*. *a*, anus; *c*, cavity (coelom) in sterile posterior genital sac; *cd*, coelomoduct; *flc*, flame-cell; *g*, gonad; *gp*, genital pore; *int*, intestine; *m*, ventral mouth; *np*, nephridiopore; *pb*, proboscis; *pp*, proboscis pore. Dorsal view.

The finer branches coming from the flame-cells have an intracellular lumen with thin wall and no cilia.

But in many genera the organ may extend backwards, even to near the anus, and a main longitudinal canal occurs collecting side-branches from the flame-cells and usually giving off numerous efferent ducts along its course (*Eupolia*, *Valencia*, *Lineus*, and others). But, as originally described by Montgomery (1897) in the freshwater *Stichostemma*



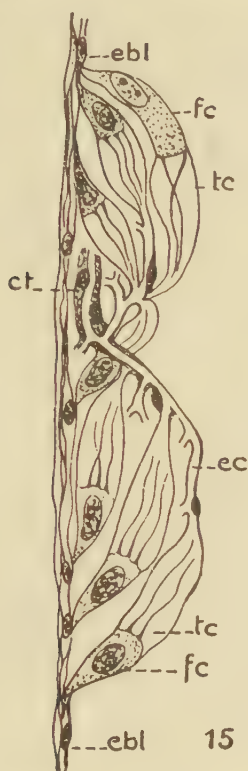
TEXT-FIG. 14.

Transition from ordinary type of flame-cell, a (*Drepanophorus*) to d, specialized type of female *Cephalothrix spiralis*. Modified from figures of Coe (1930). *ch*, terminal chamber of protonephridial canal; *cw*, wall of canal; *fl*, flame of cilia; *flc*, body and nucleus of flame-cell.

(*Tetrastemma*), there may be several separate protonephridia distributed along each side of the body. In the terrestrial *Geonemertes* there may be hundreds or even thousands of separate nephridia, each with a bunch of flame-cells, a convoluted excretory canal, and an efferent canal (Schröder, 1918; Hett, 1924, 1928; Coe, 1929). Wijnhoff (1910) and Coe (1930) have also found numerous small protonephridia, with only one or two flame-cells, in the marine *Cephalothrix* (see footnote, p. 145).

Although the development of these organs is not yet thoroughly known, the observation by Böhmig (1898) that the several separate protonephridia of the adult *Stichostemma* are joined together by a longitudinal canal on each side in the young supports his suggestion that the discrete organs have phylogenetically arisen by the subdivision of an original pair (Text-fig. 13). Such separate organs do not necessarily correspond in number and position on the two sides of the body.

Of considerable interest is the fact, originally discovered by Punnett (1900) and recently confirmed by Yamaoka (1939), that in certain species of *Baseodiscus* (*Eupolia*) some of the efferent ducts may open, not as usual to the exterior, but

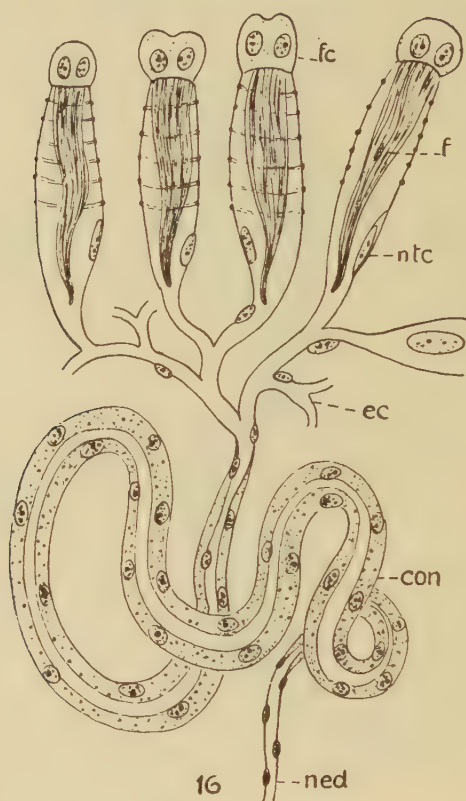


TEXT-FIG. 15.

Male *Cephalothrix spiralis*. Diagram of cephalic proto-nephridium showing flame-cells in lumen of blood-vessel (from Coe, 1930). *ct*, collecting canal; *ebl*, epithelial lining of cephalic blood lacuna; *ec*, end canal leading to flame-cell, *fc*; *tc*, terminal chamber.

into the oesophagus. This condition recalls the 'enteronephric' system of certain earthworms (p. 244); its functional significance is, however, unknown in the Nemertines.

The flame-cells may be distributed in the parenchyma below the muscle layers or near the wall of the gut; but, as already mentioned above, they are usually closely related to the main



TEXT-FIG. 16.

Geonemertes agricola. Diagram of single protonephridium (from Coe, 1930). *con*, convoluted canal; *ec*, end canal; *f*, flame of cilia; *fc*, binucleate flame-cell; *ned*, efferent duct; *ntc*, nucleus of terminal chamber.

longitudinal blood-vessels. Grouped as a rule in bunches at the ends of the slender branching canals or collecting tubules, they may push their way into the lumen of the vessel carrying its

wall with them, or actually pierce the wall so that the flame-cells are bathed by the blood.

The structure of the flame-cells varies considerably and has been studied since Bürger's work by Böhmig (1898), Schröder (1923), and more especially by Coe (1906, 1929, 1930 *a* and *b*). Often they closely resemble the solenocytes of Annelids and other forms, but the internal 'flame' seems always to consist of a number of cilia and not of a single flagellum as in typical solenocytes. The apical cell-body may have two nuclei (as in *Geonemertes*, Text-fig. 16), and may give off cytoplasmic processes. The terminal chamber, in which works the flame, may be enlarged and its very thin membranous wall be strengthened by supporting thicker bars.¹

In the female there is a series of separate small protonephridia on each side. From the external pore a narrow efferent duct leads into a thick-walled excretory ciliated convoluted canal. This narrows to a tubule which expands into a chamber close to the wall of the blood-vessel into which it may bulge. This 'end-organ' differs considerably from the usual flame-cell, since the cilia are placed on a thickening of the chamber wall containing many nuclei and surrounding the opening into the tubule. This whole structure thus acquires a superficial resemblance to the nephridiostome of an Oligochaete. Coe, indeed, speaks of it as a metanephridium opening into a coelomic cavity! But such an interpretation seems quite unjustified, and the peculiar structure can much more easily be explained as due to the spreading out of the flame-cell on the surface of the chamber, as shown in Text-fig. 14. The 'end-organ' in the female *Cephalothrix spiralis* seems to depart but little

¹ Of peculiar interest are the protonephridia of *Cephalothrix spiralis*, described by Coe (1930 *a* and *b*), in which there is sexual dimorphism. In the male there is a single anterior pair, each with a cluster of some fifty flame-cells. The finer branching canals, the collecting tubules, and the flame-cells all penetrate the wall of the lateral blood-vessel, and lie freely in its lumen (Text-fig. 15). The apex of the cell-body of the flame-cell becomes attached to the inner surface of the wall of the blood-vessel, and thus recalls the manner in which solenocytes may become fixed to the wall of the coelom in some Polychaeta, such as *Nephtys* and *Glycera* (Text-figs. 31, 34, 35).

from the usual type of flame-cell found in Nemertina and present in the male. The coelom in this phylum is surely represented, as suggested by Hatschek (1891), by the cavity of the genital sacs (see p. 124).

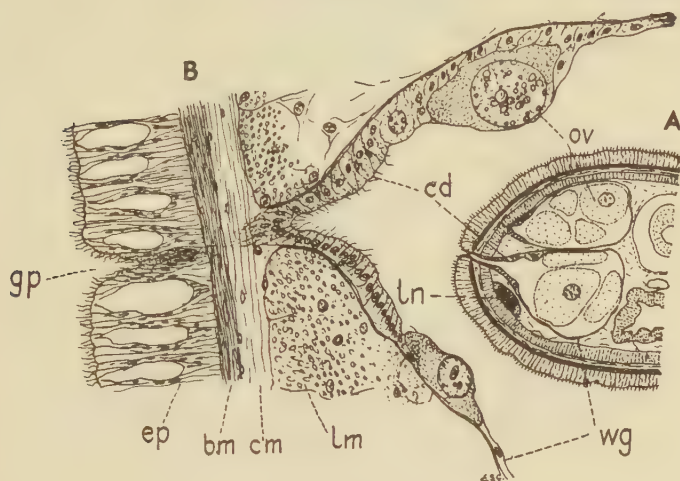
Unfortunately the origin of the protonephridia in ontogeny is not known for certain. No doubt the technical difficulties in following their development are great. Hubrecht (1886) and Bürger (1894) believed them to be derived from paired outgrowths of the presumably ectodermal wall of the oesophagus of the larva. According to Salensky (1909) the protonephridia arise from a pair of ectodermal invaginations on either side of the larval mouth. That these organs are of ectodermal origin seems most probable, but the whole question needs careful re-examination.¹

Another question requiring further study is that of the coelom in the Nemertina. Various cavities, such as the rhyncho-coel or certain transitory cavities developed in the mesenchyme of the larva or embryo, and said to become lined by epithelium (Salensky, 1909; Arnold, 1898), have been held to represent the coelom; but none of these fulfils the necessary conditions. Following Hatschek's original suggestion it was maintained (Goodrich, 1895) that the coelom is represented in the adult by the genital follicles or sacs, usually called the gonads. These generally occur in pairs alternating with diverticula of the gut along the trunk region.² At maturity each opens to the exterior above the level of the lateral nerve by a genital funnel, which grows out centrifugally from the wall of the follicle, pierces the muscular body-wall to the epidermis, and finally forms the genital pore (Text-fig. 6). This funnel, in fact, develops and functions like a typical coelomoduct (Text-fig. 17). The genital

¹ Bürger (1897-1907) states that the oesophageal outgrowths in *Lineus*, having become nipped off, come to open at the side of the mouth. The wall of the rudiment, at first thick, sends out thin-walled outgrowths to form the definitive system of excretory canals. The earlier openings being in a quite different position from that of the definitive nephridiopores must be new formations.

² This orderly arrangement in pairs along the region of the mid-gut is lost in several genera, where the genital sacs become more numerous and closely packed.

follicle, whose wall gives rise to the genital cells and the coelomoduct, clearly possesses the essential characters of a coelomic sac.¹ It may well represent a stage in the development of the coelom in metamerically segmented animals. If, while strictly



TEXT-FIG. 17.

Amphiporus lactifrons. A, Half of a transverse section of a female. B, Portion of a similar section more enlarged showing the coelomoduct, *cd*. *bm*, basement membrane; *cm*, circular muscles; *ep*, epidermis; *gp*, genital pore; *lm*, longitudinal muscles; *ln*, lateral nerve; *ov*, ovum; *wg*, wall of genital sac.

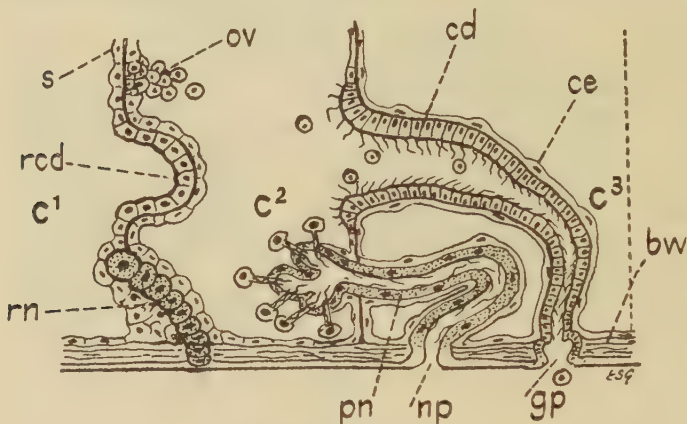
disposed in pairs they became considerably enlarged, a regular series of coelomic chambers separated by transverse septa and each provided with gonad and coelomoduct would result. Even if the genital sacs of the Nemertina may not represent actual phylogenetic stages in the development of the coelom, they certainly show how it could have arisen.²

¹ The exact relationship of the gonads to the embryonic mesoderm, and their possible development from paired coelomesoblastic bands derived from blastomere 4*d*, have not yet been clearly established.

² Although Bürger (1895, 1897-1907) appears not to have accepted this view of the homology of the genital sacs with the coelomic cavity of Annelids, he provided valuable evidence in favour of it: by showing that in some forms the sacs may grow large, and extend dorsally and ventrally

PHYLUM ANNELIDA

In this Phylum of metamerically segmented worms the 'segmental organs' are built on a fundamentally uniform plan in spite of the many specializations in the diverse Classes—Polychaeta, Oligochaeta, Hirudinea, Echiuroidea, and Archiannelida—included in it. To avoid constant repetitions in the

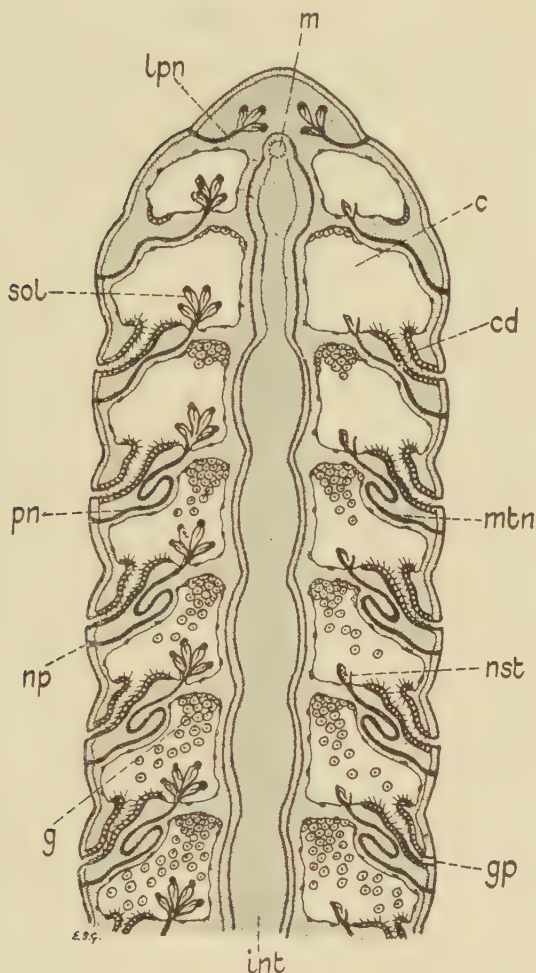


TEXT-FIG. 18.

Diagram showing relations of coelomoduct and protonephridium to coelom and coelomic epithelium in an Annelid. Three successive coelomic cavities, c^1 , c^2 , c^3 , are shown in section with intersegmental septa, s . Adult condition on right, developmental stage on left. bw , body-wall; cd , coelomoduct; ce , coelomic epithelium; gp , genital pore; np , nephridiopore; ov , ovary; pn , protonephridium with solenocytes; rcd , rudiment of coelomoduct; rn , rudiment of nephridium.

so as almost to surround the gut; that, as in *Carinella*, the genital cells may multiply pari passu with the enclosing wall of the sac, so that the organ develops as an almost solid gonad ('testis' or 'ovary'); while, in others, such as *Cerebratulus* or *Drepanophorus*, the enclosing epithelium develops first and the germ-cells enlarge and multiply later, so that there results a wide sac with a persistent cavity resembling a coelom.

Moreover, in the hindmost region of the body of some forms (*Cerebratulus*, Text-fig. 13) the sacs may remain sterile, forming neither germ-cells nor genital ducts. This specialization leads to a condition strikingly like that of so many Annelids and other Coelomates, where there is a division of labour between segments, only some of which produce gonads while the others retain only a sterile 'body-cavity'.



TEXT-FIG. 19.

Diagram of primitive Annelid in longitudinal section, showing relations of coelomoducts and nephridia to segmental coelomic cavities. Protonephridia, *pn*, on left; metanephridia, *mtn*, on right. *c*, coelom; *cd*, coelomoduct; *g*, gonad; *gp*, genital pore; *int*, intestine; *lpn*, larval protonephridium; *m*, ventral mouth; *np*, nephridiopore; *nst*, nephridiostome; *sol*, solenocyte.

descriptions given below we may take it for granted that (unless otherwise stated in special cases) this plan is as follows: They are paired excretory tubes leading from the coelom to the exterior. 'Morphologically' they occupy an intersegmental position (see p. 271). The nephridiopore is ventral, the tube or canal leading from it pierces the body-wall, and runs forwards in the coelom to the intersegmental septum which it passes through to open as a rule into the coelomic cavity of the next anterior segment by a funnel (except in immature forms and those with closed protonephridia). The funnel may be either a nephridiostome belonging to the nephridium itself (metanephridium), or a coelomostome which has been added to it (nephromixium). The post-septal nephridial canal, although it may project greatly into the coelom, remains retroperitoneal being completely covered by coelomic epithelium; so likewise are the short pre-septal canal and nephridiostome itself. The coelomostome being but a special thickened and ciliated region of the lining of the coelom is continuous at its margin with the ordinary flattened coelomic epithelium, which also covers the outer surface of its funnel, if it projects from the septum or body-wall. These fundamental relations are illustrated in Text-figs. 1, 2, 3, 7, 18, 19.

Class Polychaeta.

The Families of this Class fall naturally into two groups: Group A, with closed protonephridia, and Group B, with open metanephridia. But in both groups nephromixia may occur, and in Group B this leads to the typical mixonephridium.

Group A: with protonephridia and protonephromixia.

F. *Phyllodocidae*.—Although protonephridia with solenocytes were first discovered in *Nephtys* (Goodrich, 1897), it is in the *Phyllodocidae* that are found the most primitive and beautiful examples of this type of excretory organ.

They can best be seen in the living state without dissection in the pelagic *Alciopinae* which are generally beautifully transparent (Goodrich, 1900, 1912). *Vanadis* has a protonephridium with a long ciliated canal, curved but unbranched



TEXT-FIG. 20.

Vanadis formosa. Portion of trunk segment drawn from the living, and showing complete protonephridium and coelomoduct (genital funnel) meeting nephridial canal, but not yet opening into it (Goodrich, 1900).

at its anterior end (Text-fig. 20). Running backwards it expands slightly before opening to the exterior by the nephridiopore. Bunches of solenocytes are set at irregular intervals along the anterior region of the canal and at its tip. The tubes of the soleno-

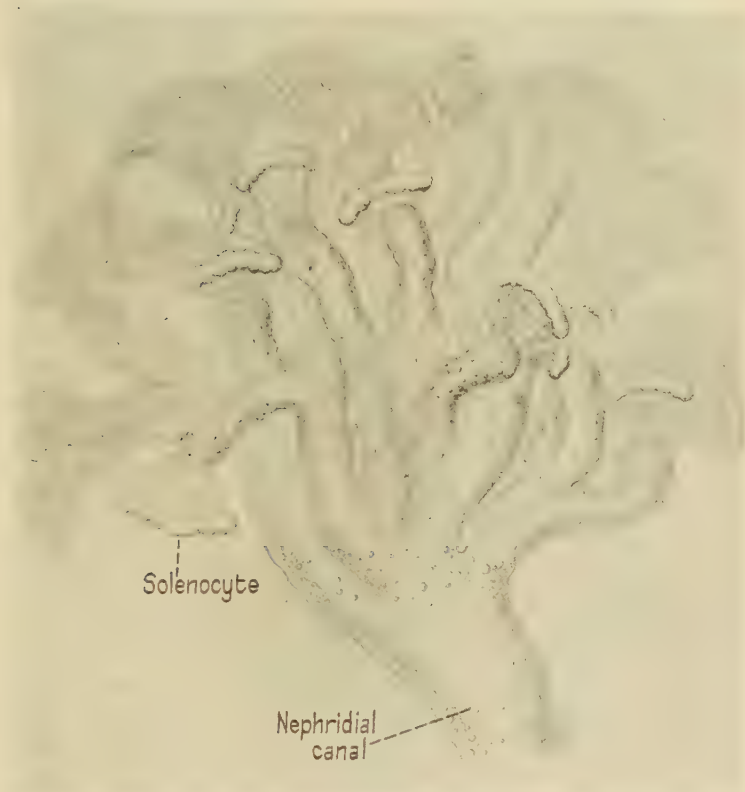


TEXT-FIG. 21.

Asterope candida. Portion of branch of canal of protonephridium, showing membrane uniting solenocyte tubes, *t*, and external cilia, *c*. From living (Goodrich, 1900).

cytes are remarkably long and narrow, and the cell-bodies of each bunch are brought together into a compact mass containing as many nuclei as there are tubes. *Alciopé*, on the other hand, has a nephridial canal with several short blind branches bearing the solenocytes at their tips. The bladder-like dilatation of the canal near the pore is more pronounced. *Asterope* has a protonephridium intermediate in structure between those

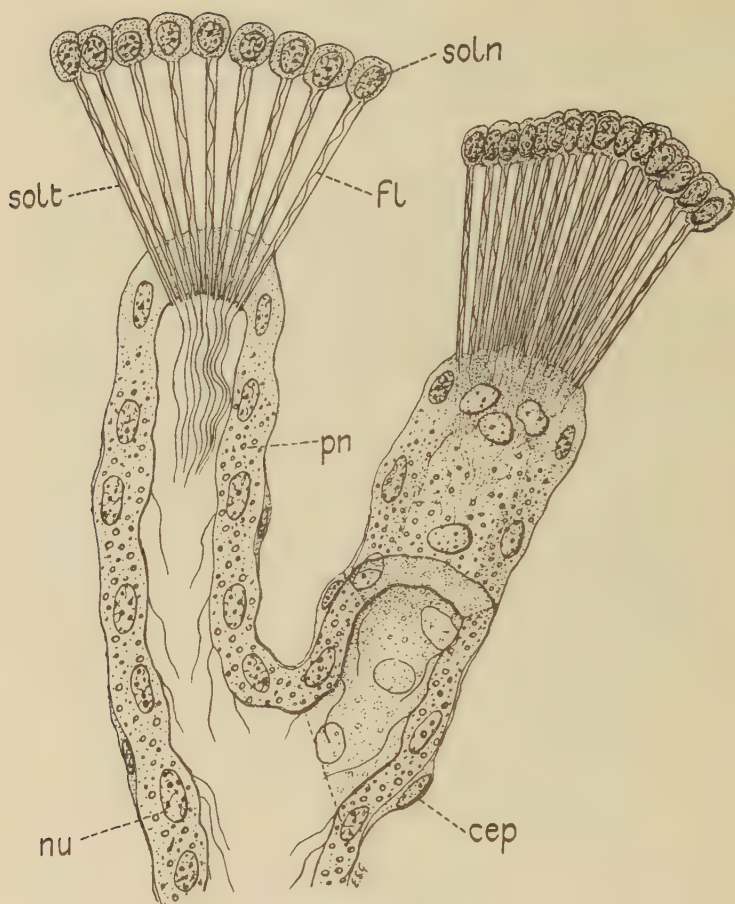
of the two previously mentioned genera. The bases of its solenocyte tubes are supported by a protoplasmic membrane (Text-fig. 21). A remarkable feature in this genus and *Alciopé* is the presence of long powerful cilia situated on the outer



TEXT-FIG. 22.

Phyllodoce paretii. Inner end of protonephridium, drawn from the living (Goodrich, 1902).

surface of the branches. They wave rapidly backwards and forwards between the rows of solenocyte tubes, which are ranged transversely, and the cilia appear to be adapted for renewing the coelomic fluid which bathes them. It is doubtful



TEXT-FIG. 23.

Phyllodoce paretii. Diagrammatic view from sections and stained preparations of two branches of protonephridium (in section on left). *cep*, coelomic epithelium; *fl*, internal flagellum; *nu*, nucleus; *soln*, nucleus of solenocyte; *solt*, tube of solenocyte.

how far the anterior ends and branches of the protonephridia of *Phyllodocids* are covered with coelomic epithelium (Text-figs. 22, 23). The solenocytes and their tubes certainly appear quite naked, but occasional flattened nuclei seem to indicate the

presence of a delicate epithelium over the whole canal, and the long cilia just mentioned probably belong to it.

The protonephridia of the Phyllodocinae, while essentially like those of the Alciopinae, are generally more branched at their anterior extremity. The solenocytes, usually very numerous, show a greater variety of structure and disposition. As a rule, their cell-bodies remain more distinct from each other, each at the free end of its tube; but in *Phyllodoce laminosa* the solenocytes are ranged in paired rows facing each other and with their cell-bodies bent down and fixed to the surface of the nephridium, slender necks of cytoplasm connecting them to the distal end of the tubes much as in *Nephthys*. Free cilia agitate the coelomic fluid between the rows.

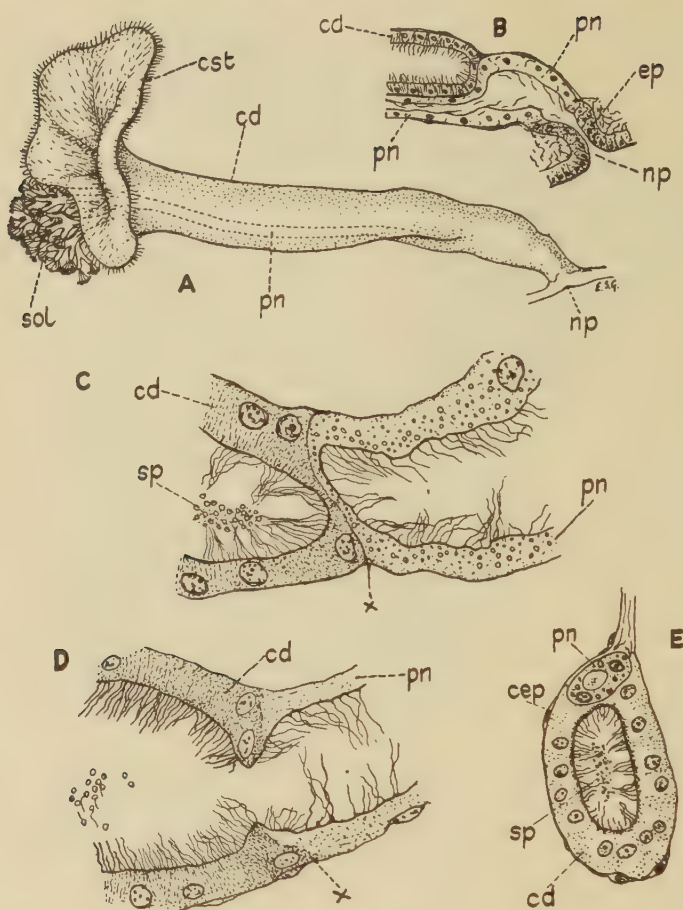
In *Eteone siphonodonta* the inner end of the protonephridium instead of bearing free branches expands into broad lobes in which the lumen of the canal branches repeatedly and forms chambers somewhat as in the Glyceridae. Rows of solenocytes plunge their tubes into these superficial cavities.¹

In all known Phyllodocids such closed protonephridia with solenocytes occur in all the segments of the body with the exception of the first few. It is interesting to note that they exist alone in a varying but rather small number of anterior sterile segments.

Obviously such an organ, without any internal opening, could not by itself act as a genital duct. Throughout the greater length of the body the segments are fertile and produce ova or spermatozoa, and in these segments the protonephridium becomes associated with a coelomostome and so acquires a widely open genital funnel (Text-figs. 1, 18, 20, 24).

This coelomostome can be observed to develop in the living Alciopinae from a patch of coelomic epithelium on the anterior face of the septum (Text-fig. 25). It becomes thickened and ciliated, then cup-shaped, and soon its blind end carrying the septum with it grows backwards along the nephridial canal to a point at which the two tubes meet and fuse. When the worm

¹ Thus, while *Eteone* approaches the Glyceridae, *Phyllodoce laminosa* resembles the *Nephthyidae* in the disposition of the solenocytes.

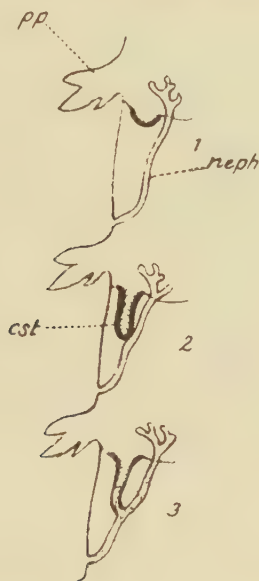


TEXT-FIG. 24.

Phyllodoce paretii. A, Reconstruction from sections of protonephromixium of mid-trunk segment of nearly mature female. B, Section of junction of posterior blind end of coelomoduct, *cd*, with nephridial canal, *pn*, near nephridiopore, *np*. *cst*, coelomostome; *ep*, epidermal ingrowth; *sol*, solenocytes. C, section of junction between coelomostome and nephridial canal in nearly ripe male *Eulalia punctifera* (Goodrich, 1900). D, similar section in ripe *Eteone lactea* (Goodrich, 1900). The communication occurs at *x*. E, *Eulalia punctifera*, transverse section showing protonephridial canal embedded in wall of coelomostome. *cep*, coelomic epithelium; *sp*, spermatozoa.

becomes genitally mature an opening breaks through at this point of fusion. The genital products are now driven by the ciliated funnel into the posterior region of the nephridial duct, and so to the exterior by the nephridiopore. This region of the excretory canal generally becomes somewhat dilated.

In *Alciope* the point of fusion is far forward and the



TEXT-FIG. 25.

Diagram of three stages in development of protonephromixium of *Alciope* (Goodrich, 1912). *cst*, coelomostome; *pp*, parapodium; *neph*, protonephridium.

coelomostome comparatively short; but in others, such as *Asterope*, it is far back and a long coelomoduct runs back to near the pore (Goodrich, 1900, 1912).

Similar coelomostomes develop in the Phyllodocinae often acquiring a very large size at maturity (Text-fig. 24). In these worms it is to be noticed that the nephridial canal as it runs along the genital funnel may become completely embedded in its wall, emerging again at its anterior end (Text-fig. 24E). The same thing happens in *Nephtys* (p. 167).

The fusion of the coelomostome with the protonephridial canal and the final break through of the lumen has been described in detail in *Eteone* and *Asterope*, see Text-figs. 26 and 24 c and d (Goodrich, 1900, 1912).

As shown above nephromixia are present in all known Phyllodocidae, and function both as excretory and as genital



TEXT-FIG. 26.

Asterope candida. Junction of coelomostome, *cst*, with protonephridial canal, *nd*. In A separating walls reduced to thin partition, in B break through has taken place. Drawn from living (Goodrich, 1912).

ducts.¹ How these nephromixia may have arisen in phylogeny will be discussed on p. 197.

F. Tomopteridae.—The excretory organs of the Tomopteridae are of peculiar interest. It is to A. Meyer, 1926, 1929, 1930, that we owe their first complete description. Only

¹ Fage (1906) has studied a large number of Phyllodocids confirming these observations and extending them to other species. He gives an excellent description and figures of the arrangement of the solenocytes of *Eulalia*, where the tubes are joined basally by a membrane and external cilia occur. *Notophyllum* is similar; but the solenocyte cell-bodies are here covered with delicate processes.

fragmentary accounts of these organs had been given by the older authors, and more recently by Fullarton, 1894, and Apstein, 1900.

Meyer has shown that usually in all the ordinary post-oral segments, except the first few, there is a pair of protonephridia with coelomostomes attached, and forming in both sexes a nephromixial complex very similar to that of the Phyllodocidae. The straight ciliated retroperitoneal nephridial canal opens to the exterior by a ventral pore near the base of the parapodium. Its inner blind end bears small solenocytes generally adhering in groups.¹

Near the inner end of each protonephridium is a small rounded coelomostome leading by a short ciliated duct into the nephridial canal. The funnel is usually composed of 8 cells with 8 nuclei and 8 radiating ciliated ridges on its coelomic surface. Several points of interest remain to be noted. In some (*Tomopteris anadyomene*) the coelomostome is absent in the first two post-oral segments leaving only the protonephridium. In most species the two organs persist throughout life (from the sixth post-oral segment), the coelomostome apparently functioning as part of the excretory apparatus. In the male sex at maturity the spermatozoa pass through the open funnel into the swollen nephridial canal to the exterior. The solenocytes may then degenerate and the tubes, &c., fall off into the coelom. The nephromixium is thus reduced to a simple mixonephridium-like organ, but it is one derived from a coelomostome and a truncated protonephridial duct. Such simple open organs occur apparently in both sexes throughout adult life in certain species (*Tomopteris elegans* and *Eunaptèris eucheta*) where no solenocytes are found in the adult.

In the females short wide ciliated funnels take the place of the usual nephromixium in the fourth and fifth post-oral seg-

¹ As described by Meyer these solenocytes differ considerably from the ordinary type in related worms. The slender tubes bear at the outer end a knob of cytoplasm, sometimes with processes, which contains no nucleus, and appears to have no 'neck' connecting it with a basal nucleated region on the wall of the canal, such as is found for instance in *Nephthys*. Moreover, the internal 'flame' is said to be composed of several cilia.

ments of most species (in segment 5 only in *Tomopteris planctonis*). They probably represent the coelomostomes only of these segments, though Meyer believes them to be special formations (see p. 203). These genital funnels carry the relatively large ova to the exterior through ventral pores.¹

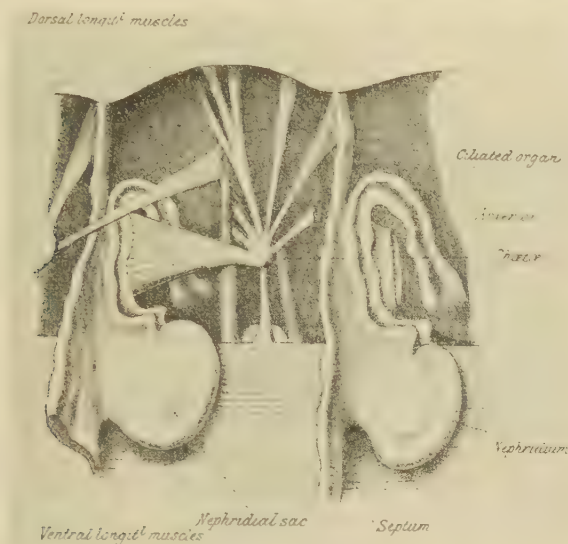
On the whole the nephromixia of this Family closely resemble those of the Phyllodocidae. But, in the fourth and fifth post-oral segments of the female, the protonephridial element of the complex appears to be much reduced, and the two pairs of oviducts are formed mostly, if not entirely, by the enlarged coelomostomes and their short ducts. A similar division of labour and corresponding specialization of structure takes place among the nephromixia of many Polychaeta.

F. *Glyceridae*.—The allied Family *Glyceridae* is of great interest. The nephromixial complex in *Glycera* is composed of a closed excretory protonephridium with solenocytes, and a coelomostome which apparently never opens either into the protonephridium or to the exterior (Goodrich, 1898). These nephromixia occur in every segment except some 15–20 at the head end and a few at the tail end. They are attached to the body-wall ventrally by the remains of the septa much reduced so as to allow free passage of the coelomic fluid from segment to segment. The nephromixia are built on the same plan in all known species of *Glycera*, differing only in details and the relative development of the parts.

The lip of the coelomostome is usually (*Glycera unicornis*, *Glycera siphonostoma*) drawn out into dorsal and ventral projections, and is continued to form a deeply grooved prolongation running to the body-wall where it merges into the general coelomic epithelium (Text-fig. 27). The mouth of the coelomostome leads to a blind sac due to the bulging backwards of the septum where the funnel develops (Text-fig. 28). It has been named 'nephridial sac' (Goodrich, 1898), but would

¹ The *Tomopteridae* are luminous, and it is a remarkable fact, according to A. Meyer (1929), that the coelomostomes in certain segments in some species become converted into luminescent organs, the so-called 'rosette organs'. Such organs, usually composed of eight radiating cells, do not open to the exterior, and secrete fatty globules.

more appropriately be called 'phagocytal sac', since it belongs not to the nephridium but to the coelomostome, and serves to receive the leucocytes and débris driven into it by the ciliated epithelium of the extensive funnel, which epithelium also penetrates into the sac itself. The sac is small in *Glycera convoluta*, larger in *Glycera unicornis*, and best developed



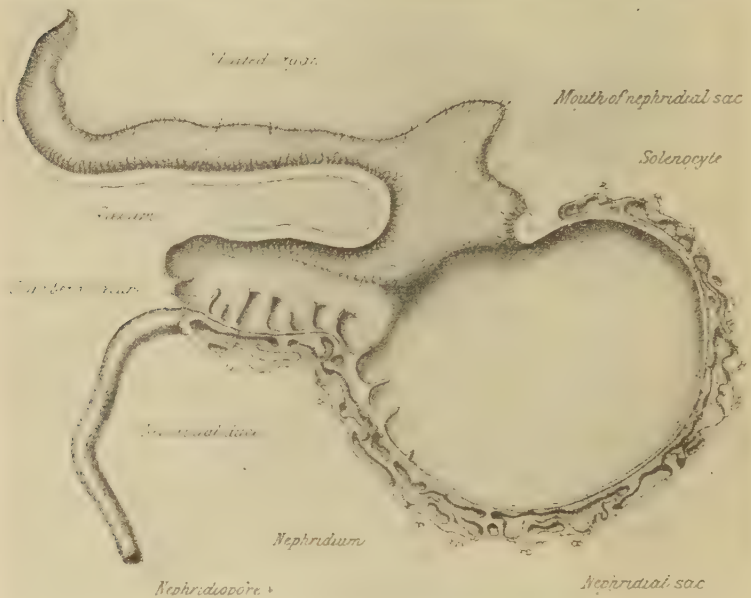
TEXT-FIG. 27.

Glycera unicornis dissected to show protonephromixia in two trunk segments, dorsal view (Goodrich, 1898).

in *Glycera siphonostoma*. In the two latter species it is further provided with a caecal outgrowth incompletely divided into chambers by ingrowth of the wall. This caecum extends along the nephridial canal, and probably represents the posterior end of the funnel which fuses with and opens into the canal in those other forms, see *Goniada* below, where a genital funnel is fully developed and functions as such. Here, in *Glycera*, the coelomostome is reduced to the condition of a 'ciliated organ'—part of a ciliophagocytal mechanism (see p. 200). Unfortunately, the shedding of the genital products

does not yet seem to have been actually observed, presumably they escape by rupture of the body-wall (see p. 201).

Very characteristic are the protonephridia of *Glycera* (Goodrich, 1908). From its ventral pore the nephridial canal runs inwards to the septum in front, passes through it, and projects into the coelom as a compact syncytial mass in which the



TEXT-FIG. 28.

Glycera siphonostoma. Reconstruction of a protonephrium cut in half, showing coelomoduct forming ciliated organ, 'nephridial' sac, and caecum (Goodrich, 1898).

lumen branches repeatedly forming a sort of sponge-work spreading over the phagocytal sac described above (Text-figs. 28, 29, 30). The primary branches give off secondary arborescent branches which at intervals expand into chambers near the coelomic surface. Situated over these chambers are the scattered solenocytes projecting freely into the coelom. The tube of each solenocyte opens into the chamber, its flagellum passes

into the cavity.¹ A few cilia are present in the secondary branches, and numerous longer cilia in the primary branches



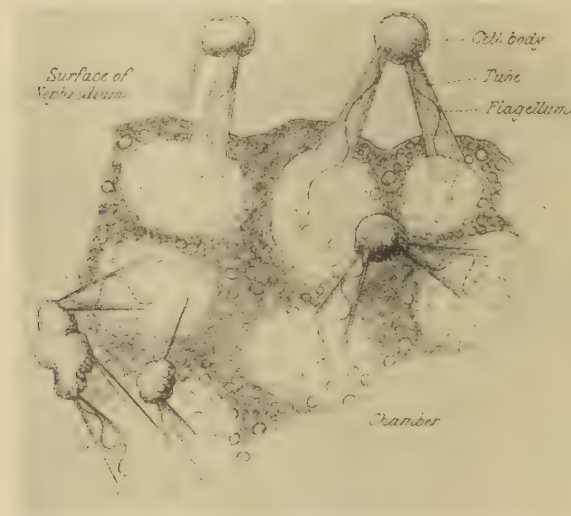
TEXT-FIG. 29.

Glycera unicornis. Surface view of portion of protonephridium showing branching canal and solenocyte chambers with oval apertures for tubes, *apt*, but solenocytes not drawn (Goodrich, 1898).

¹ The solenocytes are usually set in groups of from two to five with their cell-bodies joined together for mutual support. Their tubes are conical with narrow distal and expanded fixed end. Delicate longitudinal flutings strengthen the wall of the tube which is often compressed and oval in section (Text-figs. 29 and 30). In *Glycera unicornis* the large cell-bodies, containing each an oval nucleus, come together in pairs (Text-fig. 31) and bend downwards to become fixed to the surface of the nephridium and remain connected with the distal ends of the tubes by elongated necks, much as in *Nephthys*. A similar arrangement has been described by Fage (1906) in *Glycera alba*. He also figures the lip of the coelomo-

and canal leading to the pore, all tending to drive fluid to the exterior. The syncytium is loaded with excretory vacuoles and granules of a yellowish colour.

The genus *Goniada* shows a more primitive condition



TEXT-FIG. 30.

Glycera convolutus. Surface view of living protonephridium (Goodrich, 1898).

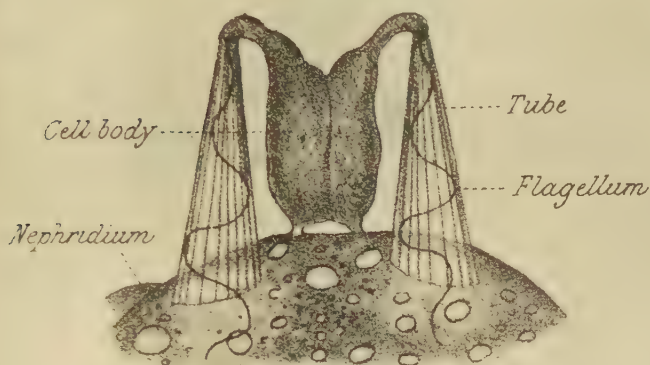
(Goodrich, 1898). The protonephridium here resembles that of the Phyllodocids, with rows of solenocytes set along short branches of the canal and external cilia. Fage (1906) has given a good description and figures of it in *Goniada emerita* from living material. The coelomostome develops rather late, and in the hinder fertile region of the trunk greatly enlarges at maturity. Its posterior end then fuses with and opens into the

stome in *Glycera tessellata* as rounded and devoid of the usual prolongation towards the body-wall.

Whether the protonephridia of Glyceridae are always covered by a continuous layer of coelomic epithelium is doubtful; nuclei are scarce and only the solenocytes project freely into the coelom for certain.

nephridial canal (Text-fig. 32). The genital products thus pass to the exterior just as in Phyllodocids (Goodrich, 1898).¹

It would be interesting to know the structure of these organs in the genera *Hemipodus*, *Eone*, and *Hemiglycera*; but they have not yet been described. It is clear, however,



TEXT-FIG. 31.

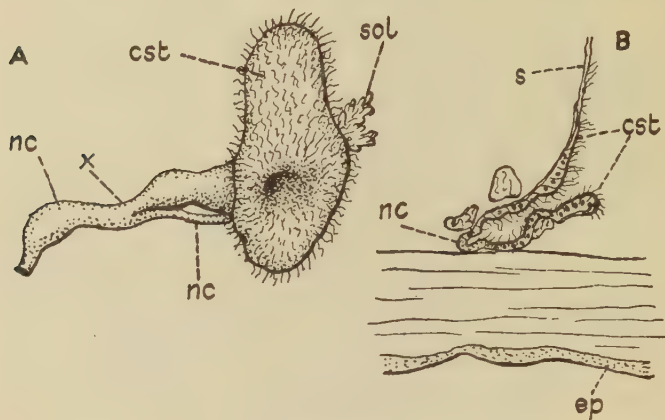
Glycera unicornis. Two solenocytes on surface of living protonephridium (Goodrich, 1898).

that in *Glycera* the genital funnel is 'degenerate' and has been converted into a 'ciliated organ' (see p. 200).

It has recently been shown by Lubischew (1915) that there may be several nephromixia per segment in *Glycera* (Ehlers had apparently observed them, but mistook them for ovaries). In *Glycera capitata* from Mourman he describes from three to eight nephromixia on each side per segment, disposed

¹ As already mentioned, although the mode of exit of the genital products does not seem to have been observed in other Glycerids, it is highly probable that they escape by dehiscence at maturity in those genera where the coelomoducts have become reduced to 'ciliated organs' in the 'cilio-phagocytal' complex. *Goniada* is the only genus so far known to have preserved the more primitive structure and function of the coelomoduct.

either separately or in bunches. Sometimes, at all events, the nephridial canal bifurcates (see also *Nephthys*, p. 169). The presence of many nephridia in one segment is common among the higher Oligochaeta, and has been described by Eisig in *Capitella* (1887). It would be interesting to know whether in



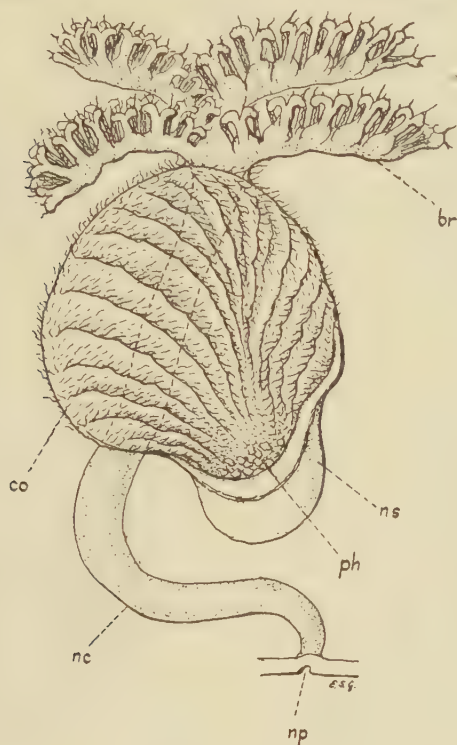
TEXT-FIG. 32.

Goniada maculata. A, Reconstruction from sections of a protonephromixium of ripe male (Goodrich, 1898). B, Longitudinal section showing coelomostome, *cst*, opening into protonephridial canal, *nc*, protonephridium, *ep*, epidermis; *s*, septum; *sol*, solenocytes; *x*, junction of coelomoduct with protonephridium (Goodrich, 1898).

Glycera also it is due to a secondary splitting up of the original paired rudiments (p. 194). But the similar multiplication of the coelomoducts has not before been described in Polychaeta, and is known in one case only in Annelida.

F. *Nephthyidae*.—The single genus *Nephthys* is placed in a Family having affinities with both the Phyllodocidae and the Glyceridae. This is evidenced by the presence of protonephromixia consisting of coelomostomes in the form of 'ciliated organs' closely associated with protonephridia provided with solenocytes. It was in *Nephthys* that solenocytes were first discovered, and that protonephridia were first shown to exist throughout the trunk segments (except the first few) of an adult Polychaete (Goodrich, 1897).

These protonephridia are of remarkable structure. The slender canal coming from the ventral pore passes through the body-wall, enters the septum, and reaches the posterior surface of the 'ciliated organ' (Text-fig. 33). Passing through the wall

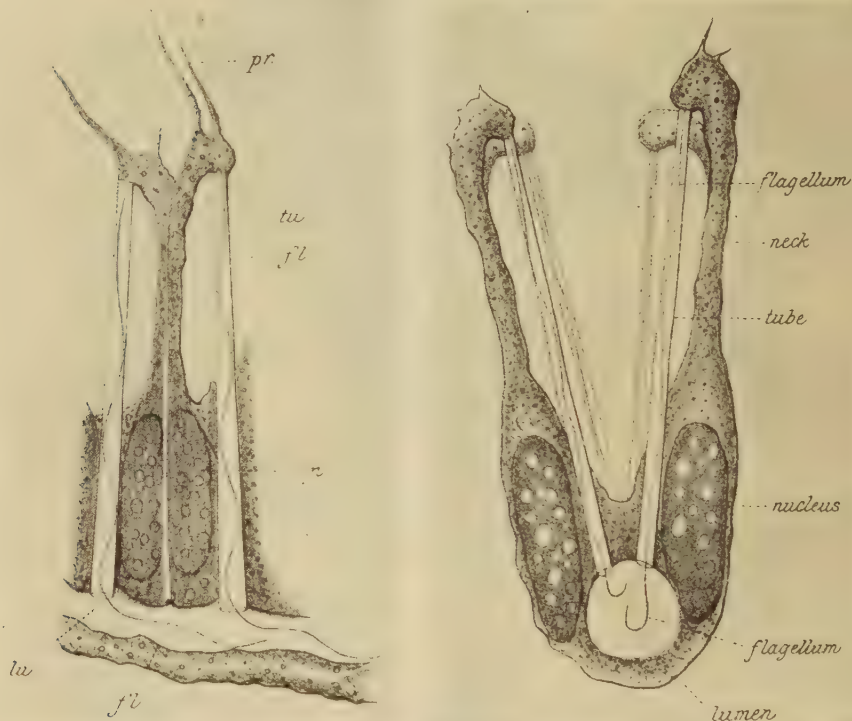


TEXT-FIG. 33.

Nephthys caeca. Reconstruction of a protonephromixium, showing protonephridium with coelomostome = 'ciliated organ', *co*, overlying canal, *nc*. *br*, branch of protonephridial canal with solenocytes; *np*, nephridiopore; *ns*, 'nephridial' phagocytal sac; *ph*, phagocytes.

of this organ the canal emerges again and divides into several branches (from 2 to 6) projecting freely into the coelom of the preceding segment. The branches end blindly, and along them are set the solenocytes in pairs (rarely three together) in two

regular rows meeting at the extremity (Text-figs. 34 and 35). The tubes being all turned towards the inside the rows, so to speak, face each other. Each solenocyte has a swollen body fixed to the wall of the branch and containing the oval nucleus, and a long slender neck of cytoplasm which bends over to reach



TEXT-FIGS. 34 AND 35.

Nephthys scolopendroides. Optical longitudinal and transverse sections of protonephridial branch showing solenocytes (Goodrich, 1897).

the distal extremity of the tube. From this region of the neck are given off delicate tapering processes of cytoplasm of doubtful function. The proximal end of the long cylindrical tube

pierces the wall of the canal; the internal flagellum, attached at its distal end, projects far into the canal lumen. The bodies of each pair of solenocytes are closely adherent, and also the necks except at their divergent distal ends; only a fine line of separation can usually be detected between the two cells.

This arrangement of the solenocytes resembles that already described in *Phyllodoce laminosa* and *Glycera unicornis*, where the cell-bodies also bend downwards so as to become fixed to the surface of the nephridium (see p. 165).

My own observations, described above, were made on *Nephthys scolopendroides* and *Nephthys caeca*. Fage (1906) has since described protonephridia of similar structure in *Nephthys hombergii* and *Nephthys agilis*.

The coelomostome in *Nephthys* is in the form of a plate-like fan-shaped 'ciliated organ' attached laterally to the septum and body-wall near the intersegmental groove, and close to the dorsal end of the protonephridial canal (Text-fig. 33). The exposed ciliated surface has high ridges with delicate denticulated crests converging from the broad dorsal edge towards the narrower gutter-like region leading ventrally into a phagocytal pocket, or widely open sac, closely connected with the nephridial canal (Goodrich, 1898, 1900; Stewart, 1900; Fage, 1906). The whole complex forms a cilio-phagocytal organ, particularly well developed in *Nephthys caeca* (see further, p. 200).

At no stage is the coelomostome known to open either to the exterior or into the nephridial canal. How the genital products reach the exterior has not been observed. Probably they escape by bursting of the body-wall as in Nereids, since the Nephthyidae are known to have an active epitokous stage (Augener, 1912).

We may here mention the remarkable discovery by Lubischew (1915) of the multiplication of the ciliated organ in a Nephthyid and also in a Glycerid (see p. 165) from Mourman. He finds in *Nephthys ciliata*, from about the tenth segment backwards, chains of ciliated organs with their phagocytal sacs. There are usually from 10 to 16 on each side in each segment.

The protonephridia remain paired, but are unusually well-developed with as many as 11 primary and 22 secondary solenocyte-bearing branches. Lubischew points out that, strangely enough, Fedotov has described, also from Mourman, a *Protomyzostomum* with numerous coelomoducts.

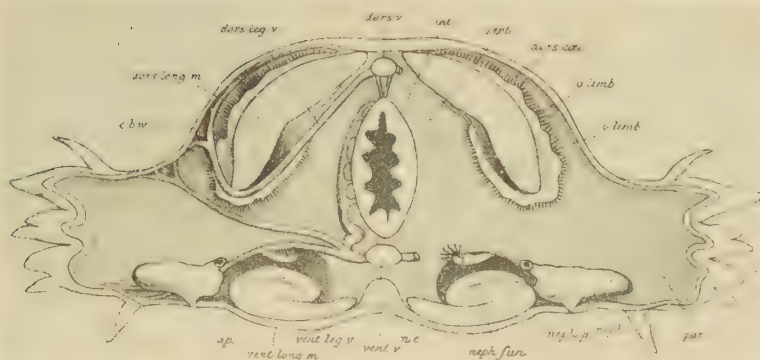
Group B. With metanephridia, metanephromixia, and mixonephridia.

Section 1. With metanephridia.

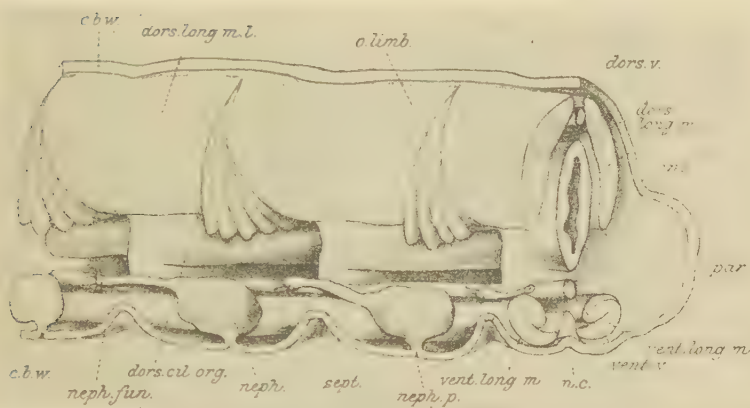
F. Nereidae.—The Nereidae (Lycoridea) are exceptional among Polychaeta in having in every segment of the body (except the first six to eight and the last few segments) a pair of metanephridia and a pair of quite separate and specialized coelomostomes ('dorsal ciliated organs', Goodrich, 1893; Fage, 1906).

The body of the nephridium is situated near the ventral nephridiopore in one segment, and its nephridiostome projects forward into the next segment (Text-fig. 36 A, B). It is suspended at the free edge of the septum which here limits an aperture allowing the coelomic fluid to flow from one segment to the other.

The well-differentiated nephridiostome, quite characteristic of the family (Text-figs. 37 A, B), is a bell-shaped funnel lined by an epithelium of almost cubical cells provided with powerful cilia which beat rapidly towards the lumen of the canal. The margin of the funnel may be everted and even reflected on to its outer surface (*Nereis dumerilii*). From this margin extends a rim of dense finely granular cytoplasm drawn out into irregular processes bearing long cilia. The number, shape, and disposition of these processes differ, each variety being characteristic of the species to which it belongs (Goodrich, 1893, 1900; Fage, 1906). The processes are but slowly motile, but their cilia move quickly in a peculiar wavy manner, apparently searching for and selecting from the cells and particles in the surrounding fluid; some of which are prevented from entering the funnel, while others are allowed to pass. Nevertheless, the processes themselves can ingest certain particles. Coelomic



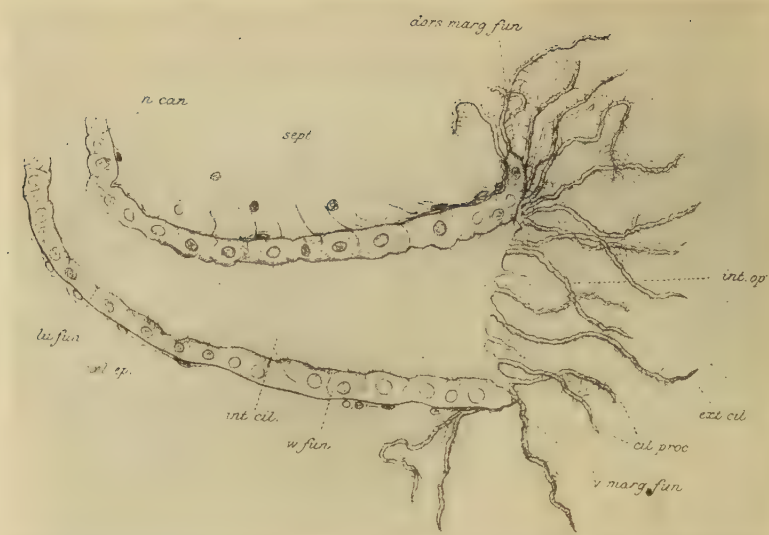
TEXT-FIG. 36 A.



TEXT-FIG. 36 B.

TEXT-FIGS. 36 A AND B.

Nereis diversicolor. A, Diagram showing posterior portion of a trunk segment seen from in front. *olimb* and *ilimb*, outer and inner parts of dorsal 'ciliated organ' (coelomostome); *dors coel*, dorsal extension of coelom; *neph*, body of metanephridium; *nephfun*, nephridiostome of metanephridium of next posterior segment; *sept*, septum. B, Left side view of trunk segments with left body-wall removed (Goodrich, 1893).



TEXT-FIG. 37 A.



TEXT-FIG. 37 B.

epithelium invests the outside of the funnel, as it does the rest of the nephridium.

From the nephridiostome extends backwards a narrow ciliated canal to the body of the nephridium, a compact mass in which the nephridial lumen is much coiled and differentiated into regions, being narrow at first and wider later. The wall of this canal is formed of a syncytium with many nuclei, contains granules and vacuoles, and cilia are distributed along it generally in a row on one or both sides. Smaller nuclei seem to belong to connective tissue cells packing the intervals between the coils. A short nonciliated region of the canal leads to the exterior through a pore in the cuticle.

Coexisting with such complete metanephridia are a pair of specialized coelomostomes, the so-called 'dorsal ciliated organs' (Goodrich, 1893). This organ is a roughly triangular area of closely ciliated coelomic epithelium, somewhat crescentic in form, and embracing the ventral edge of the dorsal longitudinal muscles (Text-figs. 36 A, B). Its margin passes into the general flat epithelium, its inner limb extends over a backwardly directed fold of the septum slung on the dorsal tegumentary blood-vessel running transversely from the dorsal longitudinal vessel. Its tapering outer limb, closely adhering to the muscles, follows the tegumentary vessel as it passes dorsally along a narrow coelomic space between muscle bundle and body-wall to near the dorsal mid-line about the middle of the segment. The coelomic ciliated surface of the organ is marked by some six to ten deep transverse grooves alternating with sharp ridges and diminishing in number towards the dorsal end of the outer limb. The ciliary current is directed towards this region, and here are accumulated phagocytes in the coelomic cul-de-sac (see p. 200).

The organ occurs in all species so far examined (Goodrich,

TEXT-FIGS. 37 A AND B.

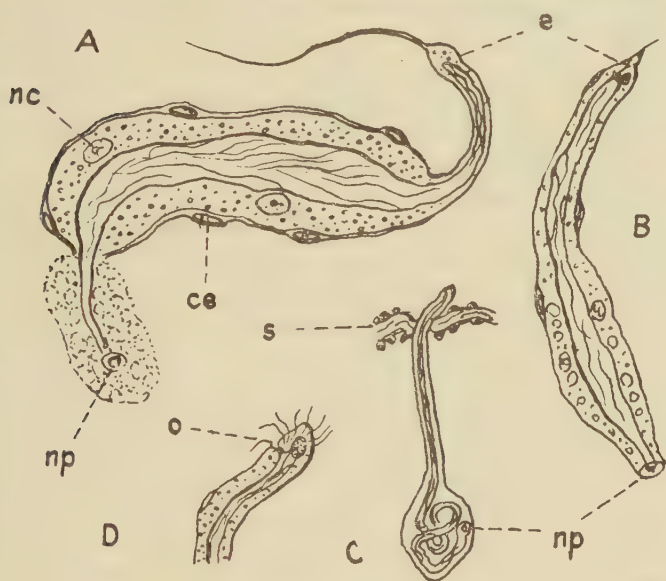
A, *Nereilepas furcata*; B, *Nereis irrorata*. Nephridiostomes drawn from the living; B, complete, A, in optical section (Goodrich, 1893 and 1900). *cilproc*, marginal ciliated process; *coelep*, coelomic epithelium; *dorsmargfun* and *vmargfun*, dorsal and ventral margins of nephridiostome; *extcil* and *intcil*, external and internal cilia; *intop*, opening into coelom; *lufun*, lumen of funnel; *ncan*, nephridial canal.

1893; Kowalevsky, 1895; Fage, 1906); but may vary somewhat in size, being particularly well developed in *Nereis dumerilii*. It appears in the young, and persists throughout life, though in the heteronereid phase it is usually reduced or absent. That this 'dorsal ciliated organ' is indeed the representative in the Nereidae of the coelomoduct or genital funnel of the Capitellidae and other Polychaeta, as originally suggested by me (1893), there can now be no doubt in the light of subsequent discoveries (see Hesionidae, and other families). But it has lost its original genital function in the Nereidae, no longer acquires an opening to the exterior, and has become converted into a 'cilio-phagocytal organ', at all events in the majority of species in which the genital products are known to escape by dehiscence (see further, p. 201). It is possible, however, that some species still exist which have no specialized epitokous stage, and that in them the coelomostomes still function as genital ducts. It is much to be hoped that zoologists having the opportunity of studying such species will consider this question. More especially would it be interesting to know how the genital products are shed in those Nereids which inhabit fresh waters.

The early development of the metanephridia of *Nereis* has unfortunately not yet been described, but E. Meyer has provided some valuable information about the nephridia of later larval stages (1887). He found, in the young *Nereis cultrifera* of about six to eight segments, a pair of small unbranched protonephridia in the third and fourth segments succeeded in the more posterior segments by pairs of more advanced nephridia leading to the metanephridial condition (Text-fig. 38 B, C, D). Each protonephridium opens by a ventral pore but has no funnel. Its inner blind end has a single nucleus and an internal 'flame' of cilia. More cilia occur in the lumen of the short canal. The extremity is prolonged into a hollow process resembling a solenocyte tube and ending in a delicate cytoplasmic process. While the nephridia of segments 3 and 4 degenerate later without opening internally, those of the succeeding segments acquire a coiled canal and a nephridiostome. A minute opening appears at the anterior pre-septal end, it

enlarges, the nucleus of the terminal cell divides, cilia project into the coelom, and so develops the adult funnel. This account, which accords with some incomplete observations of my own, clearly supports the conclusion that the funnel in *Nereis* is a true nephridiostome.

F. Hesionidae.—This is a remarkable and important



TEXT-FIG. 38.

A, Larval 'head-kidney' of *Polymnia nebulosa*. B, Larval protonephridium of *Nereis cultrifera*. C, Definitive nephridium of later stage. D, Inner end of pre-septal region of same nephridium showing piercing of nephridiostomal opening at o. *nc*, nucleus of coelomic epithelium; *e*, inner blind end of protonephridium; *nc*, nucleus of canal cell; *np*, nephridiopore; *s*, septum (Meyer, 1887).

Family since it affords conclusive evidence of the conversion of the coelomostome, serving as a genital funnel (combined with the excretory metanephridium to form a mixonephridium), into a 'ciliated organ' serving as a 'cilio-phagocytal organ' similar to that found in the Nereidae.

At one end of the series we have *Hesione* (= *Fallacia*)

where the ciliated organ was first discovered and described (Goodrich, 1897), at the other end *Irma* with mixonephridia acting both as genital and excretory ducts; and various genera provide intermediate stages.

The metanephridium of *Hesione* resembles that of *Nereis* but is simpler.¹

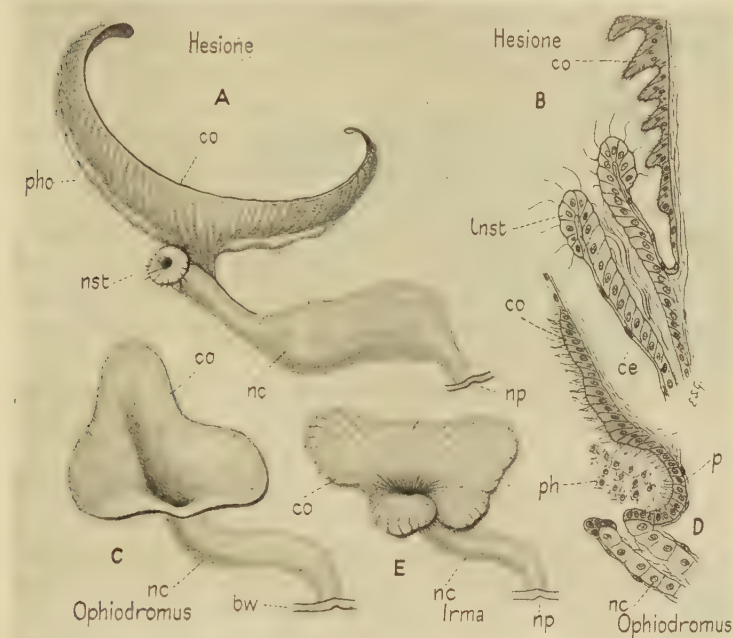
The ciliated organ is a large crescentic structure related to a dorso-lateral transverse blood-vessel, and attached to the posterior surface of oblique muscles with the curved inner and outer horns projecting freely (Text-fig. 39 A, B). Its outer surface has a large number of closely set ciliated ridges and grooves running transversely from the dorsal to near the ventral edge of the organ along which stretches an elongated phagocytal mass. Although this ciliated organ appears to be quite independent of the nephridium, it is interesting to note that from about the middle of its ventral edge a strip of its epithelium extends downwards to join the nephridiostome; and, in at all events a genitally ripe specimen, some ciliated ridges extend here also. Yet the nephridiostome in *Hesione* remains sufficiently distinct to be dissected out separately.

Turning now to the genus *Irma* (Goodrich, 1900), we find that the coelomostome (Text-fig. 39 E), though obviously corresponding to the 'ciliated organ' of *Hesione* and possessing the same ciliated ridges, is in the form of a funnel-shaped opening of the nephridium (here resembling a mixonephridium). It is firmly fixed to and surrounds the opening of the nephridial canal to which the ciliated ridges converge, the nephridiostome is suppressed, but the tissues of the two components remain histologically distinct. In young specimens the coelomostome is relatively small; but in a ripe male it is seen to be much enlarged, spreading over neighbouring blood-vessels and muscles, and well-adapted for driving the genital products to

¹ There is an elongated funnel with an everted margin bearing powerful long cilia. A 'flame' of long cilia works down the funnel itself which is formed, as in *Nereis*, of a definite columnar epithelium. There follows a narrow ciliated canal leading to the body of the nephridium where it becomes much convoluted until it passes ventrally to the nephridiopore (Text-fig. 39 A, B). The wall of the excretory canal is syncytial and ciliated.

the exterior down the short nephridial canal, which becomes dilated with sperm in the male.

While *Tyrrhena* closely resembles *Hesione*, *Kefersteinia* and *Ophiodromus* (Text-fig. 39 c) seem to occupy



TEXT-FIG. 39.

- A, *Hesione sricula*, metanephromixium reconstructed. B, *Hesione sricula*, section through nephridiostome and its connexion with 'ciliated organ' (coelomostome). C, *Ophiodromus flexuosus*, reconstruction of metanephromixium. D, *Ophiodromus flexuosus*, section through 'ciliated organ' (coelomostome) attached to inner end of metanephridium. E, *Irma latifrons*, reconstruction of metanephromixium. *bw*, body-wall; *ce*, coelomic epithelium; *co*, coelomostome or 'ciliated organ'; *lnt*, lip of nephridiostome; *p*, pocket at base of coelomostome; *ph*, phagocytes; *pho*, phagocytal organ.

an intermediate position between the two extremes. In these genera, and especially in *Ophiodromus*, the coelomostome

seems to surround the opening of the nephridium less completely than in *Irma* and chiefly on its dorsal side where a pocket is formed in which leucocytes tend to accumulate.¹ The coelomostome cells remain sharply distinguished from the excretory nephridial cells loaded with granules.

Fage (1905, 1906) has confirmed most of my observations on the Hesionidae, and has given a detailed description of the phagocytal organ of *Hesione*. He has also added to our knowledge of other genera, drawing attention to the origin of the coelomostome from the peritoneum, to its increase in size at maturity, and to the reduction of the coiling of the nephridial canal in those forms where it functions as a genital duct. Unfortunately we are still in ignorance of the mode of emission of the genital products in *Hesione* or *Tyrrhena*. Fage and myself agree that they probably do not pass through the narrow and much coiled nephridial canal, though I have found a few spermatozoa in it in one case.

This point and the question whether a ciliated phagocytal organ has been independently acquired in this family will be discussed later (p. 201).

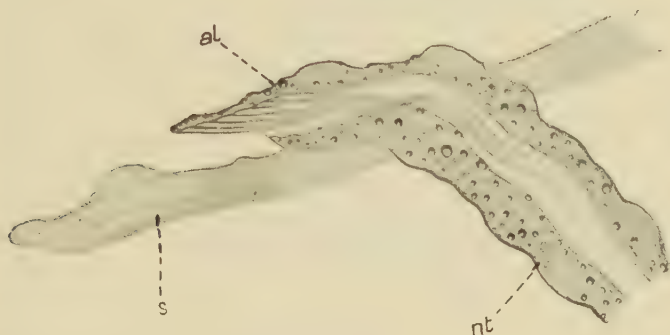
F. Syllidae.—With regard to the Syllidae, it was shown in a previous paper (Goodrich, 1900) that the conversion of the small-funnelled metanephridium into the large-funnelled organ of the mature male or female worm is not due to mere growth, as had hitherto been supposed, but to the addition to the nephridium of a genital funnel (coelomostome) derived from the coelomic epithelium.

The structure of the nephridium itself is very uniform throughout the family (Goodrich, 1900, 1930, 1933; Fage, 1906). It consists of a slender bent tube opening to the exterior by a ventral pore on one segment, and into the coelom of the next anterior segment through the septum by a nephridiostome. The lumen of the canal may be intracellular in young and small forms, or become more or less clearly intercellular. The nephri-

¹ Podarke (Gregory, 1907) is another genus of intermediate structure, where the coelomostome is fastened to the dorsal lip of the nephridial opening and forms a flattened plate with curved edges, but serves to drive the genital products down the uncoiled and expanded nephridial canal.

diostome is characteristic, with a very short lip fixed to the septum, and a projecting tapering lip bearing a bunch of long cilia forming a 'flame' working into the canal (Text-fig. 40).

Such metanephridia occur in all segments of the body except for a few anteriorly and one or two posteriorly. But, in those segments destined to become fertile and in which testes or



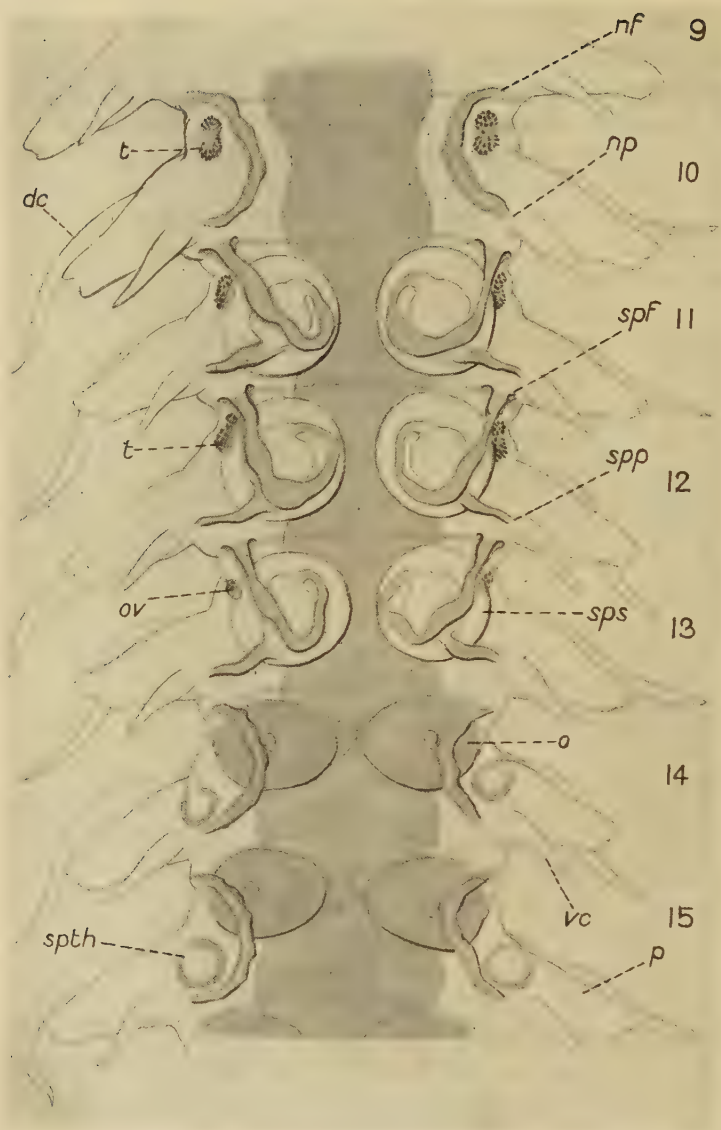
TEXT-FIG. 40.

Pionosyllis neapolitana. Enlarged view from life of unmodified nephridiostome of metanephridium of non-sexual segment. *al*, anterior lip of nephridiostome; *nt*, nephridial canal; *s*, septum (Goodrich, 1930).

ovaries are developed, there becomes grafted on to the open end of the nephridial canal a ciliated coelomostome (Text-fig. 41), and the nephromixia so formed serve at maturity as genital ducts, though the nephridial canal may also retain its excretory function. This development of nephromixia occurs also in those species in which special reproductive stolons are formed.¹

Odontosyllis enopla is an interesting case (Goodrich, 1933), for in this species the coelomostome is well-developed (even with ciliated ridges converging towards the nephridial

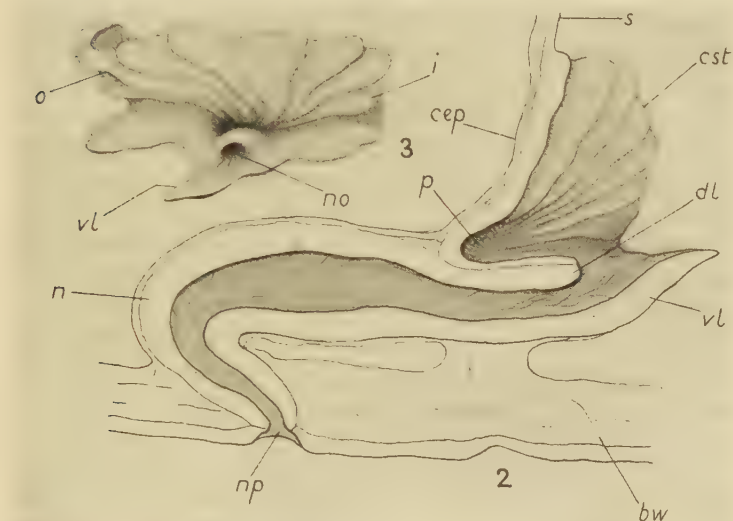
¹ The coelomostome generally begins to show early in the immature worm, where it first appears as a group of enlarged coelomic epithelium cells close to the dorsal lip of the nephridiostome (Goodrich, 1900 and 1930). This patch spreads more and more over the anterior face of the septum and soon becomes ciliated. It wraps round the nephridial opening, until finally a new large complete funnel is formed with a prominent lower lip. Usually the nephridiostome itself disappears as such in the process.



TEXT-FIG. 41.

Pionosyllis neapolitana. Diagrammatic ventral view of segments 9-15, enlarged. *dc*, dorsal cirrus; *nf*, nephridiostome; *np*, nephridiopore; *o*, large ovum; *ov*, ovary; *p*, parapodium; *spf*, spermiducal coelomostome; *spp*, spermiducal pore; *sps*, sperm-sac; *spth*, spermatheca; *t*, testis; *vc*, ventral cirrus (Goodrich, 1930).

opening), but the nephridiostome remains intact and is included in its lower lip (Text-fig. 42). Moreover, a small blind pocket is present at the bottom of the genital funnel, apparently representing the similar pocket often found associated with



TEXT-FIG. 42.

Odontosyllis enopla. Above: front view (3) of combined coelomostome and nephridiostome. Below: reconstruction of left half of metanephromixium (2). Both enlarged. *bw*, body-wall; *cep*, coelomic epithelium; *cst*, coelomostome; *dl*, *vl*, dorsal and ventral lips of nephridiostome; *i*, inner and *o*, outer margins of coelomostome; *n*, nephridial canal; *no*, opening of nephridiostome; *np*, nephridiopore; *p*, pocket at base of coelomostome; *s*, septum (Goodrich, 1933).

'ciliated organs'. Thus, in *Odontosyllis enopla*, both coelomostome and nephridiostome though closely associated are clearly distinguishable in the completed metanephromixium.¹

¹ The exact disposition of the more or less modified metanephridia, and their conversion into fully developed nephromixia varies in different species (Goodrich, 1900). In a ripe male *Pionosyllis* sp. from Naples the first fourteen setigerous segments are sterile. Opening into the fourteenth segment is a pair of well-formed but small cup-shaped coelomo-

Another interesting Syllid is the hermaphrodite *Pionosyllis neapolitana* (Goodrich, 1930). Ordinary metanephridia are present as usual, but in the three fertile male segments, 10, 11, and 12, they become greatly modified at maturity.¹ Genital funnels of coelomic origin are added to them, the nephridial canals become enlarged, somewhat coiled, and their middle regions expanded to spherical chambers with thick refringent walls (Text-fig. 41). The nephridial cells here become loaded with granules of a secretion which serves in the formation of spermatophores (a somewhat similar condition has been described by Pruvot (1902) and Fage (1906) in certain other genera).

In this species the metanephridia remain unmodified, with small nephridiostomes, in the many female segments. These segments without coelomoducts are provided with paired ovaries, and begin immediately posteriorly to the three male segments. The large ripe ova seem to emerge through the dorsal body-wall and not through the nephridia. The actual emergence of the ova has, however, not yet been observed.

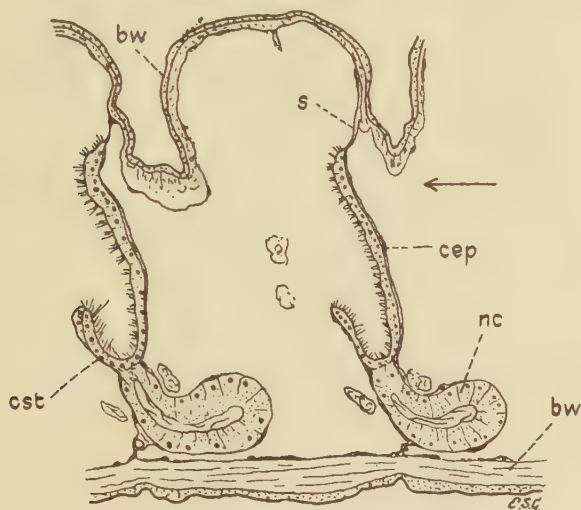
In those Syllids with an anterior sterile stock and posterior fertile stolons large coelomostomes develop only in the fertile segments. But in the stock not only do the nephridiostomes and the nephridial canals remain unmodified, but little or no trace can be seen of the coelomostomes.

Fage (1906) has confirmed these observations and conclusions, and has described several other species adding details about stomes. Passing forwards the coelomostomes become progressively smaller, disappearing about the ninth setigerous segment where they are represented by only a few coelomic cells. Twenty-five fertile segments with well-developed metanephromixia serving as genital ducts follow behind the fourteenth. Their funnels extend far over the anterior face of the septa, and also laterally on to the body-wall (Text-figs. 43, 44).

¹ That the special histological structure of the canal cells is often continued into the upper lip and the base of the lower lip of the nephridiostome, while the structure of the cells of the coelomostome is quite different (without excretory granules and vacuoles, and with closely set relatively short cilia), is also good evidence that these two funnels are of different origin. In the nephromixia of the three male segments of *Pionosyllis neapolitana* (1930) the nephridiostome can be clearly distinguished, much as in *Odontosyllis enopla* (Text-fig. 41).

the modifications undergone at maturity by the nephridial canal.¹

It has already been remarked (p. 119) that no hard and fast line can be drawn between metanephromixia and mixonephridia. In most Syllids the coelomostome becomes so closely connected to the open end of the metanephridium that the resulting organ



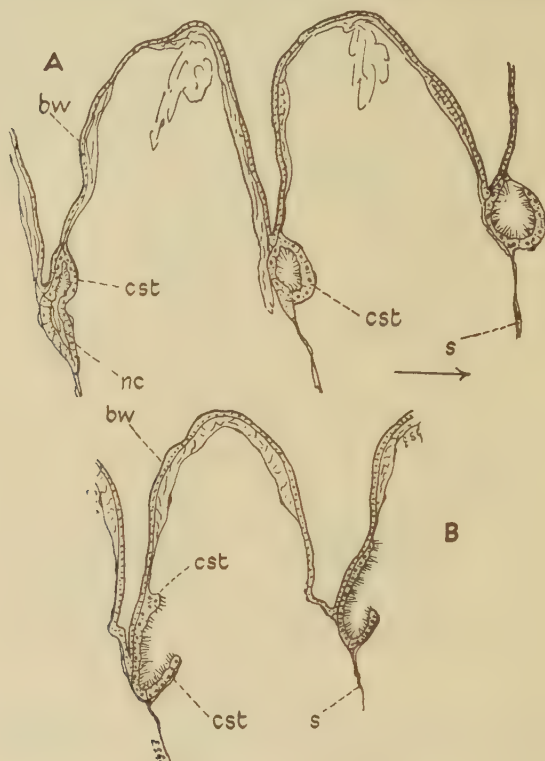
TEXT-FIG. 43.

Pionosyllis sp. ♂, longitudinal vertical section of fertile trunk segments. Arrow points headward. *bw*, body-wall; *cep*, coelomic epithelium; *cst*, coelomostome; *nc*, nephridial canal; *s*, septum. Enlarged.

cannot be distinguished in structure from the typical mixonephridium of the majority of Polychaeta here classed in Group

¹ The aberrant Polychaete, *Ichthyotomus sanguinarius*, parasitic on the Teleost *Myrus vulgaris*, and recently described by Eisig (1906), appears to emit its genital products by dehiscence in the male. Its nephridia seem to belong to the mixonephridial type, with small funnels in most segments. But into the fourth segment of the female open a pair of large ciliated genital funnels (coelomostomes) leading to ventral pores. In the male they are represented by degenerate vestigial organs which have lost their original function according to Eisig.

B (see below, p. 186). Nevertheless, the organ of the Syllid differs from the mixonephridium in that it acquires full development



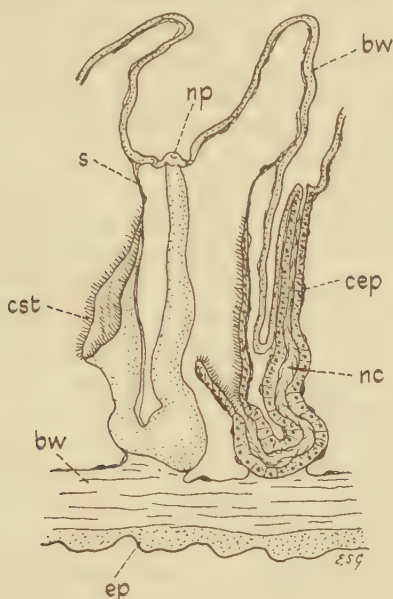
TEXT-FIG. 44.

Pionosyllis sp. ♂. Enlarged longitudinal horizontal sections of fertile trunk segments; A, more ventral; B, more dorsal. Lettering as in Text-fig. 43.

only in fertile segments and at sexual maturity, whereas the mixonephridium develops as such early and in every segment of the trunk bearing nephridia.

The remaining families of the Polychaeta lead a more or less sedentary life in burrows or tubes, and are generally grouped together as 'Sedentaria'. In the adult state they all possess

mixonephridia some of which function as genital ducts (Text-fig. 3). Metanephridia and even protonephridia (?) may also occur very rarely (p. 193); the mixonephridia may undergo interesting specializations according as they are more excretory



TEXT-FIG. 45.

Nerines sp. Longitudinal section of two consecutive segments, enlarged, left view. Showing reconstructed mixonephridium of anterior segment. *bw*, body-wall; *cep*, coelomic epithelium; *cst*, coelomostome; *ep*, epidermis; *nc*, nephridial canal; *np*, nephridiopore; *s*, septum.

or more genital in function. In the former kind the canal is most developed, in the latter the coelomostome.

Spiomorpha.—In Spionidae and Ariciidae (Attems, 1902; Eisig, 1914) where the parapodia are dorsally shifted the mixonephridia are U-shaped, with dorsal nephridiopore at one end, and large coelomostome at the other (Text-fig. 45). The marked difference in histological structure between pre-septal funnel and post-septal canal and the abrupt change at their point of

union, testify to the different origin of these two parts of the mixonephridium. Their development has unfortunately not yet been described.

A conspicuous glandular swelling of an eversible ectodermal invagination at the pore develops at sexual maturity especially in female Ariciidae (Eisig, 1914). In some Spionids described by Fage (1905, 1906), and especially by Söderström (1927) complications set in at maturity in the male where the enlarged funnel leads to one or two expansions of the canal in which spermatophores are formed.

The condition described by Allen (1904) in the Disomid *Poecilochaetus* is interesting, for here while typical mixonephridia serving as genital ducts occur in the many fertile hinder segments, the anterior sterile segments (from third to sixteenth) have apparently metanephridia only.¹

In the middle and posterior regions of *Chaetopterus* are mixonephridia serving both as excretory and genital ducts (Joyeux-Laffue, 1890).

Section 2. With mixonephridia. The next four Families are usually placed in the 'Errantia'.

F. Eunicidae.—This Family also has mixonephridia with a simple excretory canal and large trumpet-shaped coelomostome particularly well developed at maturity when it functions as a genital funnel.

First described as mixonephridia in *Eunice* (Goodrich, 1900), they have since been studied by Fage (1906) in several more genera. He figures the coelomostome of *Hyalinoecia tubicola* and *Lumbriconereis impatiens*. I find it with deep grooves on its ciliated inner surface in a ripe female of the latter genus.

¹ The nephridiostome is small, projects but little beyond the septum, and is composed of a few cells of the same histological structure as those of the actively excretory region of the canal. The genital funnel in the more posterior segments is fixed to and surrounds the inner nephridial opening, extending as usual over the anterior face of the septum and forming a prominent ventral lip. The modified coelomic epithelium cells of which it is composed have no excretory granules, but a densely ciliated surface and other characters commonly found in coelomostomes.

F. *Chrysopetalidae*.—The excretory organs of these worms have been described by Fage (1906) as typical mixonephridia in both sterile and fertile segments of the body.

F. *Aphroditidae* (*Polynoidae*).—This large and diversified Family is provided with mixonephridia which act both as excretory and genital ducts in the fertile segments (Darboux, 1900; Fage, 1906; Wiren, 1907; Storch, 1915; Fordham, 1925). They are absent in several anterior segments. The wall of the wide ciliated nephridial canal in the *Polynoinae* may be much folded and pocketed, thus increasing its excretory surface, and generally opens at the tip of a papilla (Fage). Though little is known about the development of these organs, Fage remarks that the funnel figured by Häcker (1895) in the larva is so small that it may well be a nephridiostome.

Fordham gives a good description of the coelomostome in *Aphrodite*. Its lower lip is much smaller than the extensive upper lip which spreads widely over the septum and neighbouring muscles. The ciliated surface of this lip is marked with numerous sharp radiating ridges closely resembling those of the 'ciliated organ' of *Nephtys* or *Nereis*. In *Sthenelais*, on the contrary, I find the ventral lip particularly well developed.

F. *Amphinomidae*.—A good description of the mixonephridia of *Hermodice carunculata* has been given by Storch (1914). It has a short rather wide excretory canal opening into the next anterior segment by a large coelomostome with everted margin drawn out at its inner and outer edges into tapering ciliated areas spreading over blood-vessels. Deep ciliated ridges and grooves converge towards the opening into the nephridial canal. Storch remarks on the resemblance of this funnel to the 'ciliated organ' of *Nereis*. I have since found that *Eurythae complanata* has a similar large grooved coelomostome, but a more twisted canal. *Euphrosyne* is remarkable in that the trumpet-shaped coelomostome opens backwards.¹

¹ Fage (1906) says that I was mistaken in stating that the funnel opened backwards into the same segment as the nephridiopore. A re-examination of my sections confirms my observation that it opens more backwards than forwards. Moreover, a series of longitudinal sections of an

F. *Chlorhaemidae*.—Of doubtful affinity are the remarkable *Chlorhaemidae* which have a single pair of large anterior excretory mixonephridia with greatly developed wide canal and small funnel. With these we associate the *Sternaspidae*.

F. *Sternaspidae*.—This very highly specialized family, represented by *Sternaspis* adapted for life in the sand, is generally supposed to be allied to the *Echiuridae*, but appears to be more probably related to the *Chlorhaemidae*.

Its excretory and genital organs were for long said to be quite exceptional in several ways, more especially in that they were alleged to have no communication with the coelom. However, it has been shown that this latter statement is incorrect and their real structure is as follows (Goodrich, 1897).

There is one pair of excretory organs in the form of large irregular lobed sacs applied to the oesophagus, covered with coelomic epithelium, and connected to the body-wall ventrally between segments 6 and 7 by tapering ducts which, however, appear to end blindly before reaching the surface [similar blind endings to the nephridial ducts have been described by Eisig in *Capitella* (1887)]. In *Sternaspis* these nephridia appear to be organs of accumulation, for the large cells lining the very diminished lumen are loaded with peculiar uniform granules of complex structure. Each such nephridial sac is in reality in open communication with the coelom by means of a ciliated canal ending in a small funnel situated on the aforementioned duct. Whether this funnel, with its somewhat irregular ciliated lip, is a nephridiostome or a coelomostome it is impossible to tell without knowing its development. Its appearance suggests that it belongs to the nephridium.

The genital apparatus is the same in both sexes. It consists of a lobed sac, evidently formed by the union of two in the

Amphinomid from Ceylon (unfortunately not identified) shows the same peculiarity. No great morphological importance is to be attributed to it. Probably it is due to the later shifting of the edge of the incomplete septum. No doubt the coelomostome develops as usual on the anterior surface of the septum, but in the adult may come to open dorsalwards or even somewhat backwards.

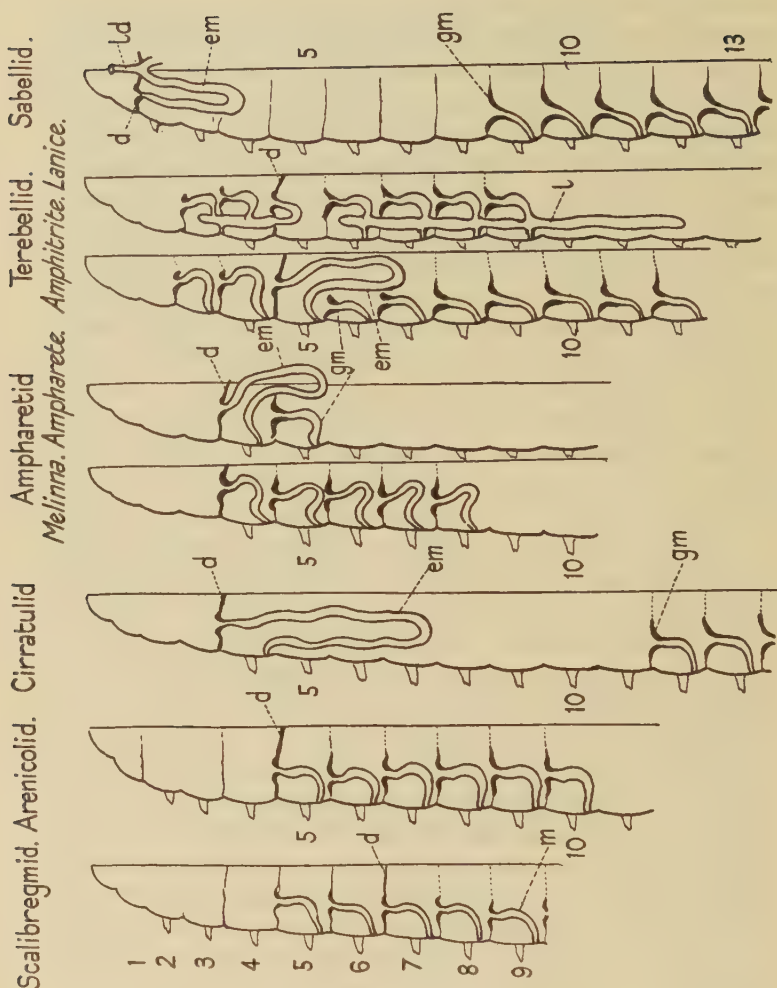
mid-line, and provided with right and left ducts passing backwards to open to the exterior at the tips of two ventral papillae on the eighth segment. On the outer side of each duct is the ciliated lip of a long narrow funnel opening ventrally into the coelom. The flat coelomic epithelium covering the whole organ is continuous at the lip with the ciliated epithelium lining the sac. The gonads are developed on blood-vessels which penetrate into the sac near the junction of the two ducts. Thus, the so-called ovaries and testes are chambers enclosing the gonads, but opening into the general coelom. No doubt they have been formed by the overgrowth of the gonadial blood-vessels by two coelomostomes. An account of the development of these organs would be of interest.

Thus *Sternaspis* would seem to show an extreme case of the specialization of the mixonephridia into anterior excretory and posterior genital, one pair of each alone remaining.

Scolecomorpha.—The Arenicolidae and certain apparently related families (Maldanidae, Oweniidae, Scalibregmidæ, Opheliidae) may provisionally be included in this group.

F. Arenicolidae.—*Arenicola* being a common laboratory type its mixonephridia, with terminal bladder and large preseptal funnel provided with a much frilled dorsal lip, must be familiar to most students of Zoology. They have been well described by Benham (1891), Gamble and Ashworth (1900), Ashworth (1904), Lillie (1905), and Downing (1909). Usually six pairs of mixonephridia are present in the adult in segments 5–10 (Text-fig. 46). A transverse diaphragm cuts off the coelom of the first four sterile segments from that of the segments of the mid-trunk region where gonads are present and the septa are reduced. The first pair of mixonephridia (sometimes reduced or absent) have relatively small coelomostomes opening through the diaphragm, and are purely excretory. The others, with large funnels, serve for the emission of the genital products but retain their excretory function as well (Text-fig. 46). The account given by Lillie of their development and the structure of the larval nephridia are dealt with below, pp. 206–9.

F. Scalibregmidæ.—The condition in the *Scali-*



TEXT-FIG. 46.

Diagram showing distribution of mixonephridia in various Families of Polychaeta Sedentaria. Dorsal views of left half of anterior region. 1, 2, 3...segments; *d*, diaphragm; *l*, longitudinal connecting duct; *ld*, longitudinal median duct; *m*, unspecialized, *em*, specialized excretory, and *gm*, specialized genital mixonephridia.

bregmidæ is possibly of importance. Ashworth (1901) has given a good description of the segmental organs in *Scalibregma inflatum*. The nephridial canal, ciliated throughout and with intercellular lumen, is bent in a loop, one branch leading to the external pore and the other coming from a small funnel of ciliated epithelium. The first three pairs of funnels open on to the anterior face of the three diaphragms (Text-fig. 46). Those of the more posterior segments are attached to the body-wall and open into the general coelomic cavity where the septa have disappeared. It may safely be concluded that these organs are mixonephridia of the usual type; but the mode of exit of the genital products is still unknown, and Ashworth believed the nephridial lumen to be too narrow to allow for the passage, at all events, of the ova.

In a more recent account of *Sclerocheilus minutus* A. and L. Dehorne (1913) failed to find even a nephridiostome in a quite small specimen, and described the later addition to the nephridium of a coelomostome. This ciliated funnel they suggested acquired at maturity an independent opening to the exterior for the emission of the genital products. Should this suggestion be verified it will provide another interesting case in Polychaetes of the opening of the coelomostome directly to the exterior,¹ such as occurs in the Capitellidae.

F. Oweniidae.—According to Gilson (1895) the nephridia (probably mixonephridia) of the Oweniidae seem to be highly specialized. In *Owenia* one (sometimes two) pairs of ciliated funnels open into longitudinal ducts in the body-wall passing forwards to pores on the sixth segment. The ducts are formed by the closing over of epidermal grooves, and serve to lead the genital products outside the closely fitting sandy tube.

¹ Incidentally these authors maintain that even in Phyllodoce the coelomostome has not been proved on the evidence of sections to lead the genital products into the nephridial canal! Clearly they are not well acquainted with the literature, and have missed my figures of *Goniada* (1898, Pl. 35, figs. 36–8), and *Eteone* (1900, Pl. 39, fig. 18), and *Eulalia* (1900, Pl. 40, figs. 23, 28–30). Most of these are here reproduced, see Text-figs. 24 c and d, 26 a and b, 32 b. Moreover, their suggestion that the function of the coelomostome is primarily excretory and secondarily genital obviously is against all the evidence.

Cirratulomorpha.—The Cirratulidae deserve to be kept apart in a special group. As described by E. Meyer (1887) they show extreme divergence between an anterior pair of mixonephridia with very long excretory canal, and the numerous posterior mixonephridia of the genital region composed almost entirely of large coelomostomes (Text-fig. 46). Interesting conditions have been described by Caullery and Mesnil (1898) in *Dodecaria concharum*. The anterior organs are as usual, but in the epitokous forms large coelomostomes develop late from the coelomic epithelium on the anterior face of the posterior septa, fuse with the epidermis, and form pores through which issue the genital products. No nephridial canal-element was found contributing to these genital ducts, and possibly they represent coelomostomes only—like those of Capitellids. Further study would, however, be necessary to establish this somewhat improbable conclusion. If the nephridium is really absent from these segments, it is probably due to secondary reduction rather than to the survival of a primitive condition not found in its allies.

Founded chiefly on the classical memoir of E. Meyer (1887), our knowledge of the mixonephridia of the remaining typically tubicolous forms is fairly complete. Various authors have added details since (Terebellids: Fauvel, 1897; Hesse, 1917; Zenkewstach, 1923. Serpulids: Chigi, 1890; Loye, 1908; Lee, 1912; Woskressensky, 1924. Hermellids: Dehorne, 1908).

Terebellomorpha.—A diaphragm separates an anterior sterile region from a posterior region of a variable number of segments where the gonads are developed and the septa disappear. The Ampharetidae (Fauvel, 1897) have the diaphragm between segments 3 and 4, and a single pair of elongated excretory mixonephridia opening through it. In *Melinna* three more pairs of similar mixonephridia follow behind. In *Ampharete* while the anterior organ is much enlarged, the posterior genital mixonephridia are represented by a single pair of short wide funnels opening on the sixth segment (Text-fig. 46).

The Terebellidae have the diaphragm between segments 4

and 5. A pair of large excretory mixonephridia open through it, and two similar pairs usually are present in segments 3 and 4. Behind the diaphragm a varying number of much shorter mixonephridia occur; in these the coelomostome is extensive and the excretory canal reduced. Their function is chiefly genital (Text-fig. 46).

An interesting fact, described by E. Meyer (1887), is that in *Lanice* the three mixonephridia opening on each side into the pre-diaphragmatic chamber have their excretory canals joined by a longitudinal connexion which opens to the exterior by a single lateral duct and pore. Posteriorly to the diaphragm the four mixonephridia present, each with large funnel and duct to exterior, similarly have their excretory canals joined longitudinally on each side (Text-fig. 46). There can be little doubt, as Meyer suggests (1888), that these longitudinal connexions are secondary.

Serpulimorpha.—The allied families Sabellidae, Serpulidae, and Hermellidae (Sabellariidae) are chiefly distinguished by the presence anteriorly of a single pair of excretory mixonephridia whose funnels open into the coelom of the first segment, while their external openings unite to a single median dorsal pore (Text-fig. 46).

E. Meyer describes this unique structure as due to the union of the two original pores in a dorsal groove of the epidermis which closes over to form a canal reaching far forwards to carry the excreta out of the tube.¹ The excretory portion of the canal is often much developed with lobes and folded wall extending back through several segments (Chigi, 1890; Evenkamp, 1931).

An observation of some significance has been noted by Malacquin (1908) who finds that in the small Serpulids *Filograna* and *Salmacina* the anterior nephridia remain in the protonephridial stage in the adult. The two protonephridia (developed from two large cells with intracellular lumen and flagellum) join as usual to a median dorsal pore but have no internal funnel. This description has been confirmed by Lee (1912), but not

¹ According to Segrove (1941) the median exit duct is formed by the junction in the mid-dorsal line of the paired canals.

by Miss Faulkner (1930). The whole question requires careful reinvestigation.¹

Group C: with metanephridia and complete coelomoducts.

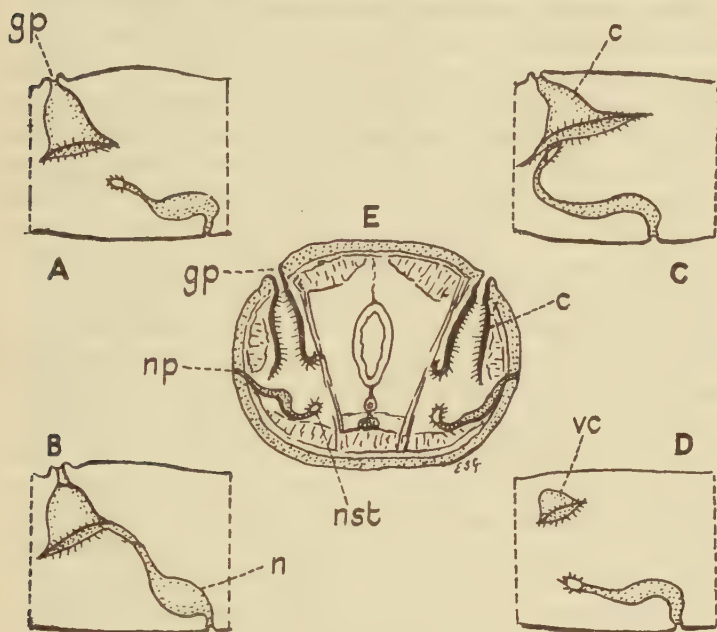
F. Capitellidae.—Of all the Polychaeta the single Family Capitellidae belonging to this Group is one of the most important from our present point of view. Eisig's fine monograph of the Capitellids of the bay of Naples (1887) gives full and accurate information as to the structure of their nephridia and genital ducts; but he failed to appreciate their morphological significance, as already pointed out (Goodrich, 1895). For this is the only Family in which the primitive segmental series of nephridia and coelomoducts can be seen side by side, often completely independent and each opening separately to the exterior. The nephridia are of the metanephridial type, with small ciliated nephridiostome, coiled canal, and lateral pore² (Text-fig. 19 on right, Text-fig. 47 E). Sometimes, as Eisig has described in *Capitella* and '*Clistomastus*', several pairs of nephridia may occur in each segment owing to the secondary subdivision of the original pair.

During the growth of Capitellids there is a marked tendency

¹ Possibly Malaquin examined young specimens in which the coelomostomes had not yet joined the nephridia. Shearer informed me that the coelomic funnels in some Serpulids may develop quite late.

² The nephridiostome may be either spoon-shaped as in *Dasybranchus*, drawn out into two points as in *Capitella*, or rounded as in *Notomastus*. The edge of its lip bears fine selective cilia, while a flame-like bunch of powerful cilia beats inside it. The organ may be little twisted, or form a compact body, containing the slender coiled canal with packing connective tissue. The nephridium may be spread over the body-wall and retroperitoneal in position, or it may bulge more freely into the lateral chamber of the coelom. A pair of such metanephridia occurs primarily in every segment, and although in the young worm (*Capitella*) they occupy the usual position, with funnel in one segment and body and pore in the next behind, yet it is characteristic of Capitellids in general that later each metanephridium comes to lie in one segment only (owing probably to the great reduction of the septa). They are usually yellowish in colour, contain many excretory granules, and are exclusively excretory in function. On the whole these metanephridia closely resemble those of the Nereids.

for the anterior nephridia to degenerate and disappear, being progressively replaced by others in more posterior segments. To a less extent this happens in many other Polychaeta. Pro-



TEXT-FIG. 47.

Capitellidae. Diagrams A, *Notomastus latericeus*; B, *Notomastus profundus*; C, *Dasybranchus caducus*; D, *Notomastus (Clistomastus) lineatus*; E, Diagram of transverse section of *Notomastus latericeus* showing relation of nephridiostome, *nst*, and coelomostome, *c*. (From Eisig's figures.) *gp*, genital pore; *n*, metanephridium; *np*, nephridiopore; *vc*, vestigial coelomoduct.

visional and definitive nephridia can thus be distinguished. The latter rarely persist even in the last one or two thoracic segments (*Mastobranchus*), but usually in all abdominal segments except some of the most anterior.

Even more interesting and important are the genital funnels described by Eisig (*Genitalschläuche*) which occur in pairs in a varying number of consecutive segments in the mid-region of

the body (generally in the last one or two of the thoracic and a larger number of anterior abdominal segments; in *Capitella* only one pair occurs in segment 8). The genital funnel of the adult is a laterally compressed bell-shaped ciliated coelomoduct, with a wide coelomostome opening downwards into the lateral chamber of the coelom, and a short conical outer end embedded in the body-wall where it meets the epidermis. At sexual maturity this extremity and the epidermis are pierced laterodorsally to form the genital pore, which allows the genital products to escape to the exterior. Except for a slight connexion of the lip of the coelomostome with that of the nephridiostome in some species, the metanephridium and the coelomoduct are quite independent organs with quite different functions.¹

Moreover, the reduction of the coelomoducts on the one hand and of the metanephridia on the other hand takes place independently; so that anterior segments may occur with genital funnels only, intermediate segments with both genital funnels and nephridia, and posterior segments with metanephridia only.

Eisig believed that the genital funnel was developed from the nephridiostome, and was thus a much enlarged and specialized portion of the nephridium which had become secondarily more or less independent. But, when we remember that a genital funnel may be present in a segment preserving no trace of a provisional nephridium, that the series of nephridiostomes remains uniform and unchanged whether the segments contain genital funnels or not, how slight and variable in position is the

¹ In *Dasybranchus caducus* there are about fifty pairs of genital funnels, from the last or penultimate thoracic segment, containing at most only vestiges of provisional nephridia. In the abdominal region they coincide with definitive nephridia. The nephridiostome is independent of, but close to, the drawn out anterior corner of the coelomostome. In *Notomastus latericeus* (Goodrich, 1900), and in *Capitella* also, the nephridiostome has no connexion with the coelomostome. But, in *Dasybranchus gajolae* where there are genital funnels only in the last two thoracic and first two or three abdominal segments, the nephridiostome becomes connected to the anterior corner of the coelomostome. On the other hand, in *Notomastus profundus*, where there are about from five to twenty pairs of genital funnels in the abdominal region, the nephridiostome is joined to the posterior corner of the lip of the coelomostome (Text-fig. 47).

connexion of the two funnels even when it does occur, and that they are known to develop independently in *Capitella*, there seems to be nothing in favour of this theory. Further, when we consider that in other Polychaeta genital funnels and nephridiostomes are known to have quite different and independent origins, the former from the coelomic wall and the latter from the nephridia, it becomes clear that Eisig's hypothesis cannot be accepted, and that on the contrary the association of the two funnels is secondary (Goodrich, 1900).

A further point of particular interest remains to be mentioned. It has been explained above when dealing with the Glyceridae, Nephthyidae, Nereidae, and Hesionidae, that the genital products may cease to be discharged through the coelomoducts and escape through the ruptured body-wall. In such cases genital pores are not pierced and the coelomostomes become modified for other purposes as 'ciliated organs'. Now, as shown by Eisig, the same sort of degeneration of the coelomoducts occurs in *Notomastus* (*Clistomastus*) *lineatus* where the genital products escape by dehiscence from the abdominal region (see p. 173).

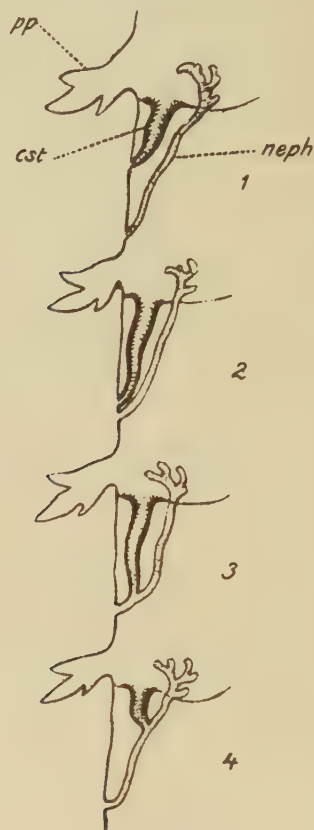
We conclude that, specialized as they are in some respects, the Capitellidae are primitive in that alone among the Polychaeta they retain the original segmental series of genital coelomoducts distinct from the nephridia. Although in some the coelomostome and the nephridiostome may become connected no really compound nephromixium is formed.

NEPHROMIXIA.

It may be asked how could the combination of two originally distinct organs (nephridium and coelomoduct) to form a nephromixium have arisen in the course of phylogeny?

In the case of the protonephromixia of Phyllodocids, for instance, it has been suggested (Goodrich, 1912) that at first both the protonephridium and the coelomoduct opened separately to the exterior, ventrally near the base of the parapodium. That the excretory and genital pores came to open closer together until they combined to form one urinogenital aperture,

and that next the coelomoduct came to meet and open into the base of the protonephridial canal. Lastly, that the meeting-

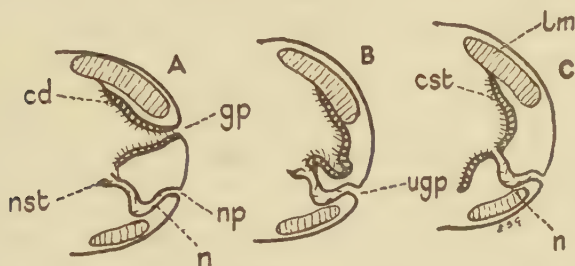


TEXT-FIG. 48.

Diagram of four possible phylogenetic stages in the combination of coelomoduct, *cst*, and protonephridium, *neph*, to form proto-nephromixium of a Phyllodocid (Goodrich, 1912). 1, Primitive conditions with separate organs. 4, Final condition with proto-nephromixium.

place of the duct and canal shifted farther and farther up the canal (Text-fig. 48). The genital products would thus be able to avail themselves of the ready-made nephridial canal to reach the

exterior, and the coelomoduct would be correspondingly shortened, the genital funnel being formed chiefly from the coelomostome. It must be remembered that in these Polychaetes the genital funnel develops late and reaches full size only at maturity. Thus, we imagine, the whole protonephromixium, as we know it in living forms, could have evolved by a series of stages every one of which was functionally efficient.



TEXT-FIG. 49.

Diagram of three phylogenetic stages from A with independent coelomoduct, *cd*, and metanephridium, *n*, through nephromixia B and C to completed mixonephridium. *cst*, coelomostome; *gp*, genital pore; *lm*, longitudinal muscles; *np*, nephridiopore; *nst*, nephridiostome; *ugp*, urinogenital pore.

In the case of Polychaetes provided with metanephridia it is possible that the metanephromixium was built up by some process similar to that just described; but it seems on the whole not improbable that a different expedient was adopted in the Hesionidae and Syllidae. We know (p. 196) that in Capitellids the nephridiostome may become connected with the anterior or posterior lip of the coelomostome. This connexion seems to lead no farther in this Family, and no completed nephromixium is developed. But, in Hesionids (p. 175), every stage seems to be represented between such a slight connexion (in *Hesione*) and the complete grafting of the coelomostome on to the nephridiostome (in *Irma*),¹ so that a metanephro-

¹ It is not suggested that the existing genera of the Hesionidae (*Hesione*, *Ophiodromus*, *Irma*), mentioned here and described elsewhere (p. 176), form a phylogenetic series. Indeed, we do not know whether they started from an ancestor provided with mixonephridia still

mixture is formed in which the genital products take a short cut and pass down the whole length of the metanephridium, the original genital pore being suppressed (Text-fig. 49). The same mode of combination may have occurred in the Syllids (p. 178), the nephridiostome being surrounded by the lip of the coelomostome. Whether this explanation is also applicable to the formation of the typical mixonephridium of the majority of the Polychaeta it is not possible to determine on our present evidence. These hypotheses are illustrated in the diagrams in Text-figs. 48 and 49.

THE CILIOPHAGOCYTL ORGAN.

In several families of Errant Polychaetes the coelomoduct loses its original function as a genital duct, and at the same time acquires the new function of gathering together floating coelomic corpuscles loaded with waste products, and so clearing the coelomic fluid of excretory matter. This modified form of coelomoduct was first discovered in the Nereidae (Goodrich, 1893), and named 'dorsal ciliated organ' (for description, see p. 173). Later, similar 'ciliated organs' were described in Hesionidae, Nephthyidae, and Glyceridae (Goodrich, 1897, 1898, 1900). It has now been clearly established that such 'ciliated organs', which do not open to the exterior, represent coelomoducts (and particularly their coelomostomes) modified for the purpose of collecting excretory phagocytes usually at a point close to the nephridium. It is interesting to note that this modification, entailing both change of function and loss of communication with the exterior has apparently been independently acquired in several families. For, in the Hesionidae and Glyceridae genera occur in which the genital funnel is fully developed and open at both ends, and the typical nephromixial connexion of coelomoduct with nephridium is completed. Moreover, it should be noted that the 'ciliated organ' occurs not only in Nereidae and Hesionidae, which are provided with metanephridia, but also in Nephthyidae and Glyceridae having only possessing well-developed nephridiostomes (as in some Syllids, p. 178), or with some less completed nephromixium with independent excretory and genital pores such as suggested for the Phyllodocid series.

protonephridia. Now, in all these cases both sexes at maturity become filled with genital products and undergo a more or less pronounced metamorphosis into epitokous forms which swarm to the surface of the sea and shed ova or spermatozoa by dehiscence. The genital products thus escaping by rupture of the thin and easily torn body-wall, genital ducts are no longer necessary.¹

Thus, while the parent is sacrificed, the advantage is presumably gained in that fertilization is more certainly secured than in ordinary reproduction.²

Not all epitokous Polychaetes shed their genital products by dehiscence. The Syllidae (p. 179), the Pacific Palolo worms among Eunicidae, and the Cirratulid *Dodecaria* (p. 192), all emit them through their enlarged mixonephridia, and possess no specialized ciliophagocytal organs.

In the Nereidae and other forms where the coelomostome is modified into a 'ciliated organ' an accumulation of phagocytes occurs in connexion with it.³

The ciliophagocytal organ is well developed in *Hesione* (Goodrich, 1897; see p. 176), and its phagocytal mass has been

¹ A similar change has occurred in the Capitellid *Clistomastus* (Eisig, 1887), where the genital products are shed by dehiscence, and the coelomoducts are degenerate and no longer form external pores.

² Epitoky has been fully observed in the Nereidae; but, although *Glycerids* and *Nephthys* are known to undergo some change at maturity, the natural shedding of their genital products seems never to have been actually witnessed. However, Mr. D. P. Wilson informs me that dehiscence occurs when ripe specimens are brought into the laboratory at Plymouth.

³ Already in 1889 Kowalevsky had noticed that in *Nereis cultrifera* cells containing brownish granules occur in paired segmental dorsal 'glands'; and that, if indigo-carmin be injected, corpuscles loaded with the dye are gathered in these 'glands'. When the 'ciliated organ' itself was discovered (Goodrich, 1893), I concluded that these cells were collected from the coelom by the action of its cilia, which produced a dorsally directed current, and that there was no real 'gland'. Later Kowalevsky (1896) again held that in addition to the accumulated phagocytes there were cells produced in the lymphoid gland. Neither Willem and Minne (1900) nor Fage (1906) found such a 'gland'. Cuénot (1902), who named the whole complex 'organe cilio-phagocyttaire', held that probably the phagocytal mass contained both gathered coelomic corpuscles and cells proliferated in it.

well described by Fage (1906) in *Hesione pantherina*. The 'ciliated organ' is very large (Text-fig. 39A) and the phagocytal mass extends all along its base, supported by a fold of coelomic epithelium passing below and outside it; the phagocytes are partly held in a meshwork of cells in the groove so formed. *Nephthys* (Text-fig. 33) possesses a well-defined phagocytal mass at the base of the 'ciliated organ' (Stewart, 1900) in a pocket-like fold of epithelium (Goodrich, 1900). Fage (1906) describes it in detail in *Nephthys scolopendroides* as composed of a network enclosing granular eosinophil cells, basophil granular cells, and a few large macrophages. Some of the cells may multiply by division. The waste substances are probably digested and passed in solution into the wall of the adjacent nephridial canal.

But it is in the Glyceridae that the ciliophagocytal organ attains its highest development (p. 160). Here, the 'ciliary organ' is usually large with an outer lip extending towards the body-wall, and an inner lip surrounding the opening of the phagocytal pocket, now a rounded sac (Text-fig. 28). This sac named the 'nephridial sac' (Goodrich, 1898) would be better called the phagocytal sac; since, although closely connected with and partly surrounded by the nephridium, the association is secondary. In *Glycera siphonostoma*, where the complex is best developed, the internal epithelium lining the sac is folded to form pockets, especially in a caecal prolongation along the nephridial canal. The sac becomes filled with coelomic phagocytes (leucocytes and haemoglobinous haematocytes) enclosing excretory granules and debris of all kinds. If the worm be injected with carmine and Indian ink, the nephridial canal takes up the carmine in solution, and the insoluble particles are carried into the sac.

Thus, in these various Families, the function of the coelomoducts has been completely changed, from organs destined to the collection and expulsion of the genital products to organs adapted to the collection of waste material.¹ No doubt the

¹ That the 'ciliated organ' is homologous with the genital coelomostome has been fully established. They never both occur in the same segment. Not only have we Families, like the Hesionidae and Glyceridae, in which

change was brought about gradually, and transition stages are not difficult to conceive. Since the new function is useful throughout life, the ciliophagocytal organ is found to develop early and persist continuously, whereas a genital funnel usually appears late, reaches its maximum at sexual maturity, and may wax and wane with the seasons.

Theory of A. Meyer.—A. Meyer (1926) found in the Tomopteridae (see p. 158) that the post-oral segments (except the first few) are provided with nephromixia, each consisting of a protonephridium with solenocytes and an attached coelomoduct (his gonostome of series 1), that (as with the similar nephromixia of the Phyllodocids) these organs function as gonoducts in the male; but that in the genital segments of the female only two larger funnels are present and serve as oviducts (his gonostome of series 2). He concluded that these oviducts belonged to a new series of coelomoducts, independently developed and not homologous with the first series.

Also, within the Tomopteridae, he traced a degenerating series of species in which the inner end and solenocytes of the protonephridial component of the nephromixium may (in both sexes) disappear, leaving a simple open tube consisting of the protonephridial canal and its attached coelomostome, as in *Tomopteris elegans*. Neglecting the far simpler explanation that some such change has taken place in the two

the passage from one to the other can be observed, but corroborative evidence can be obtained from a study of the histological structure of the two organs. Characteristic of the 'ciliated organ' in Nereidae, Hesionidae, and Nephthyidae, is the folding of the densely ciliated surface of the coelomic epithelium forming deep grooves separated by high ridges which direct the current towards the base of the organ where corpuscles are accumulated. These ridges may be drawn out into a sharp jagged edge (Goodrich, 1893, 1897). Similar ridges, serving to direct the genital products to the nephridial canal, occur on the densely ciliated inner surface of the coelomostome (genital funnel) of the nephromixia of many Polychaeta, such as *Irma* among Hesionidae, *Odontosyllis* among Syllidae. *Eurythoe* among Amphinomidae (Goodrich, 1933), some Eunicidae and Terebellidae, and the Tomopteridae. This epithelium seems to be neither glandular nor excretory, and its action is merely mechanical.

genital segments of the females, he nevertheless maintains that the oviducal funnels belong to a second series.

Extending his conclusions to other Annelida he further insists that no protonephridium can acquire an opening of its own into the coelom, and that, therefore, all metanephridia are necessarily nephromixia in Polychaeta, Oligochaeta, and Hirudinea (when upholding this view A. Meyer had apparently forgotten that Vejdovsky in Oligochaeta (1884, 1888-92), and E. Meyer (1887) in Nereis, had described in detail the formation of just such an opening—see p. 174). Speculating further, he concluded that the metanephridia of these Annelids are always nephromixia (compounded of protonephridium and gonostome series 1), and that when, as in Capitellidae, Oligochaeta, and Hirudinea, separate gonoducts occur as well, these must belong to the new second series (gonostome series 2)! A. Meyer went even farther, and maintained that in such a form as *Arenicola* the nephromixium is composed of three elements: the nephridium forming the canal, the reduced gonostome of series 1 forming the metanephridial opening, and the gonostome of series 2 added to it to enlarge and complete the funnel.

His interpretation of the metanephridium of the Oligochaeta as a nephromixium seems to be based chiefly on the more than doubtful statement of Bergh (1899) that the marginal cells of the upper lip of the nephridiostome of *Criodrilus* are derived from the coelomic epithelium. Adopting the still more speculative conclusion that the nephridial funnel of *Lumbricus*, with its numerous marginal cells set round a large central cell, represents the primitive type of funnel among Oligochaeta, where the whole upper lip (including central and marginal cells) represents the gonostome of series 1; he concluded that from this *Lumbricus* type a degenerating series with diminishing number of marginals can be traced through *Haplotaxis* and *Lumbriculus* to such forms as *Tubifex* and *Stylaria* (see further, p. 269).

It need hardly be pointed out that this theory of the history of the nephridiostome is against the teachings of comparative anatomy, and the evidence of embryology. Indeed, this whole

fantastic edifice of speculation has been severely shaken, if not actually overthrown, by A. Meyer's (1929) own later account (confirming Vejdovsky) of the development of the whole metanephridium of *Tubifex* (both canal and funnel) from a single rudiment—the nephridioblast (see p. 269, Text-figs. 74, 76).

Development of Adult and Larval Nephridia.

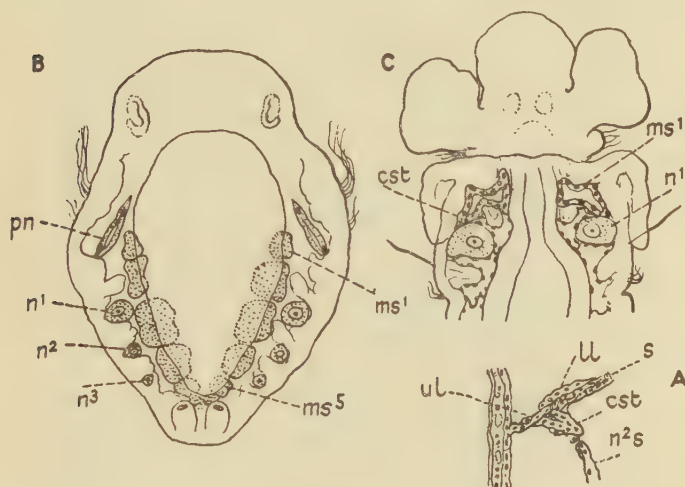
It is much to be regretted that so little has been recently published on the early development of the definitive nephridia of the Polychaeta, no doubt owing to the great technical difficulties involved. We still have to depend on the excellent work of E. Meyer (1887-8), who showed that in tubicolous forms, such as *Psygmobranchus* (*Protula*) and *Polymnia*, the post-septal excretory canals are developed from a series of intersegmental nephridioblasts while the preseptal ciliated funnel is derived from the coelomic epithelium on the anterior surface of the septa (Text-fig. 50). Each nephridioblast, at first close to the epidermis and independent of the mesoblastic somites, divides to form a chain of cells within which an intracellular lumen becomes hollowed out. The anterior blind end of this canal fuses with the posterior wall of the next somite in front now possessing a coelomic cavity (Text-fig. 50 A). The lumen of the canal becomes intercellular by the multiplication of the cells forming its wall; and breaks through at its point of junction with the funnel (which develops backwards from the coelomic epithelium of the somite) thus coming to open by a coelomostome. It also breaks through to the exterior posteriorly where it has fused with the epidermis. Thus (although Meyer did not perceive the true significance of his observations) is formed from two originally independent rudiments the complete mixonephridium of the adult, an organ not to be confused (as it so often has been and still is) with a metanephridium.¹

¹ Just as in *Polygordius* (p. 225) so in the Serpulid *Psygmobranchus* there seems to be some doubt as to the exact correspondence of nephridia and segments in larva and adult. E. Meyer describes in the larva of *Psygmobranchus* four consecutive nephridioblasts on each

R. S. Lillie studied the development of the nephridia in *Arenicola cristata* (1905); but, in spite of the excellence of his figures and the care with which the work has obviously been carried out, his results are not altogether satisfactory. He traced the origin of the nephridial tube to little masses of intersegmental tissue which he believed to be mesoblastic, but failed to find defined nephridioblasts: 'The nephridium simply becomes gradually differentiated out of an originally uniform and homogeneous mesoblast which in early stages presents no definite cell-boundaries' (Lillie, p. 384). This mass containing many nuclei is distinguished where the septum joins the body-wall at a stage when the coelom is already present. Near the central nucleus appears 'a minute space . . . the first indication . . . of the nephridial lumen'. The opinion of Lillie, who held that this cell 'is entirely similar to adjoining purely myoblastic cells, even to the possession of muscle fibres in its interior', can scarcely be accepted since, when cell-limits appear, it becomes separated as a purely nephridial excretory cell from the myoblastic cells of the somatopleure and the covering of coelomic epithelium cells. Therefore, I venture to interpret this cell as a nephridioblast occupying the usual intersegmental position between adjacent somites, although it has not been distinguished as such in the earliest stages, and its first origin is still unknown.

The nephridium which develops from this single cell is side (see Text-fig. 50B). The first pair gives rise to the larval proto-nephridium (head kidney). The second pair, which he reckons to belong to the second somite, in the course of development shifts to a position in septum 2/3, and not in septum 1/2, as we should expect. Yet at a later stage the canal which develops from this nephridioblast is said to join the funnel growing back from septum 1/2; consequently, according to Meyer, the completed adult mixonephridium opens into the coelom of segment 1 (developed in the first coelomesoblastic somite). Unfortunately, in this Serpulid the following two pairs of nephridioblasts disappear in late larval stages, so that this conclusion cannot be further confirmed. It seems possible, however, that the first adult coelomic cavity attributed to segment 1, is really that derived from the larval somite 2. This is a point which requires elucidation. On the other hand, the shifting backwards of the nephridioblast may be merely a specialization due to the large size the nephridium acquires in the adult.

described by Lillie in the later larva as a simple tube with a syncytial wall containing many nuclei and an intercellular lumen. Posteriorly the nephridium is fused with the epidermis, but does not yet open to the exterior. Anteriorly it opens for-



TEXT-FIG. 50.

A, *Polymnia nebulosa*, developing anterior mixonephridium. *n²s*, extremity of nephridial canal growing forward to join coelomostome, *cst*, growing backward from septum, *s*; *ll* and *ul*, lower and upper lips of coelomostome. B, *Psygmobranchus protensus* (*Protula tubularia*) dorsal view of larva, and C, ventral view of anterior end of later stage. *ms¹, ⁵*, coelomesoblastic somites; *n¹-³*, nephridioblasts; *pn*, protonephridium (from A. Meyer, 1887-8).

wards into the coelom through the septum. Cilia pass through this opening, but there is no nephridiostome projecting from the septum. Now, I have already described (Goodrich, 1900, Pl. 42, fig. 49, here reproduced as Text-fig. 51) in the pelagic post-larval stage of *Arenicola* a projecting funnel with a more dorsal longer lip bearing delicate cytoplasmic ciliated processes and a shorter more ventral lip without cilia (observations since verified by Ashworth in *Arenicola marina*, 1904). From its close resemblance to the nephridiostomes of

various Polychaeta and Oligochaeta I concluded that it is a true nephridiostome, and the question now arises as to what is its relation to the familiar large funnel of the definitive organ



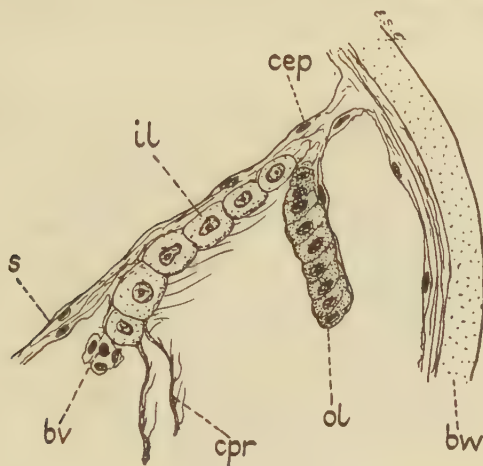
TEXT-FIG. 51.

Nephridiostome of a living post-larval stage of *Arenicola*, *cp*, showing ciliated processes; *nc*, nephridial canal (Goodrich, 1900).

well described by Gamble and Ashworth (1900), Ashworth (1904), and Lillie (1905).

According to Lillie the funnel of the adult arises mostly if not entirely from the coelomic epithelium of the anterior face of the septum the cells of which become cubical and ciliated,

although there may be a small contribution from the nephridial cells where coelomostome and nephridium meet. An examination of sections of my late post-larval stages shows that the more dorsal lip of the funnel is undoubtedly formed of nephridial



TEXT-FIG. 52.

Arenicola sp., transverse section of late post-larval pelagic stage through developing funnel of mixonephridium. *bv*, blood-vessel; *bw*, body-wall; *cep.*, coelomic epithelium; *cpr*, ciliated process of nephridiostome; *il*, inner lip (formed by nephridial cells); *ol*, outer lip (formed by coelomic epithelium), future large ciliated coelomostome; *s*, septum. Enlarged.

cells, bearing the ciliated processes at the edge, but covered externally by coelomic epithelium and with a minute blood-vessel between (Text-fig. 52). The more ventral lip is made of a double layer of coelomic epithelium of which the cells of the inner layer are already closely packed and columnar, ready to become converted into the ciliated epithelium of the coelomostome.

Lillie has described the terminal vesicle as derived from the posterior region of the nephridial canal with little or no invagination of the ectoderm at the pore.

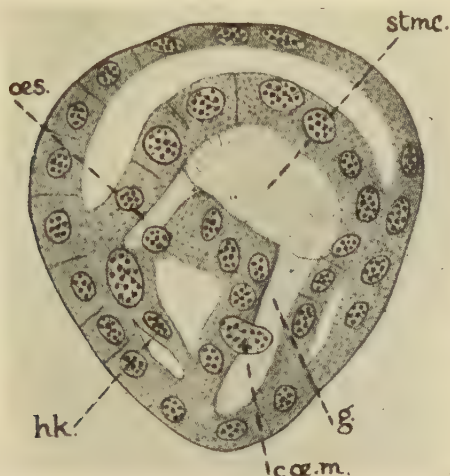
Thus the whole organ of the adult *Arenicola* develops as a typical mixonephridium formed by the combination of an open metanephridium with a coelomostome, and there seems

to be nothing in Lillie's description which is incompatible with the view that the nephridium itself is derived from a single cell, a nephridioblast, lodged at first between two consecutive mesoblastic somites. This interpretation (not adopted by Lillie) would agree with the findings of E. Meyer in other Polychaeta mentioned above.

Provisional larval 'head-kidneys' have been found in the trochophore larvae of several Polychaeta (Terebellidae, Serpulidae, Nereidae). Although so little has been done on the early development of the segmental organs of the adult, a good deal is now known about the structure and development of these larval nephridia. The work of the earlier observers was somewhat incomplete and indefinite. Hatschek (1886), Salensky (1882, 1883), and von Drasche (1884, 1885) considered them to be of mesoblastic origin, without however clearly distinguishing between coelomesoblast and ectomesoblast. Wilson (1892) attributed an ectodermal origin to a pair of cells which appear to give rise to the nephridioblasts in *Nereis* (also Iwanoff, 1928, in *Hydroides*).

The larval head-kidneys are now known to be simple protonephridia, composed of few cells pierced by an intracellular lumen closed by a flame-cell bearing a long internal flagellum and often one or more tapering external processes. The whole organ projects into the head-cavity of the larva, a space not of coelomic but of pseudocoelic origin. E. Meyer (1887-8) gave a detailed description and figure of the larval protonephridium of *Polymnia*, and showed that in *Psygmodon* (*Protula*) it is developed from the first of a segmental series of nephridioblasts budded inwards from the larval ectoderm (see p. 205 and Text-fig. 50 B). Since then Shearer (1911) has described the structure and development of the larval protonephridium in *Hydroides* (*Eupomatus*). It arises from a nephridioblast of ectomesoblastic origin, which divides to form the whole organ, and comes to open (at first according to Shearer) not as usual directly to the exterior, but into the ectodermal proctodaeum. In *Pomatoceros* (Segrove, 1941) it opens to the exterior near the anus.

It is clear, more especially from the work of Shearer, that the larval protonephridium is not of coelomesoblastic origin. Indeed, it may be formed and functional before the telomesoblast cell has begun to divide. Whether we call the nephridioblast from which the protonephridium is developed ectodermal or ectomesodermal is rather a matter of taste than of fact.

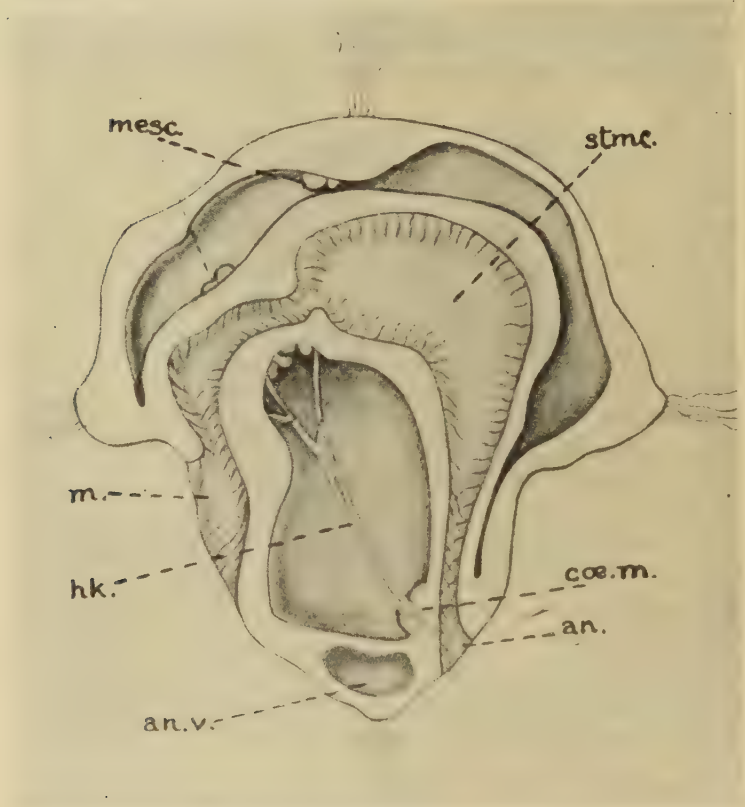


TEXT-FIG. 53.

Hydroides uncinatus (Eupomatus). Section of early trochophore, showing rudiment of 'head-kidney' with two nuclei, *hk*, and part of large nucleus of coelomesoblastic teloblast of left side, *coem*; *oes*, oesophagus; *g*, gut; *stmc*, stomach (Shearer, 1911).

They develop from a pair of large ectomesoblastic cells on either side of the oesophagus far from the two primary coelomesoblastic cells or teloblasts which are still undivided and related to the endodermal gut-wall (Text-fig. 53). Each nephridioblast divides forming a strand, two nuclei moving to the inner end and one to the base near the anus. These three cells form the whole protonephridial 'head-kidney' (Text-fig. 54). The strand becomes syncytial and hollowed out by an intracellular lumen, in which develops a long flagellum springing from below the terminal nucleus. This end-cell is attached to

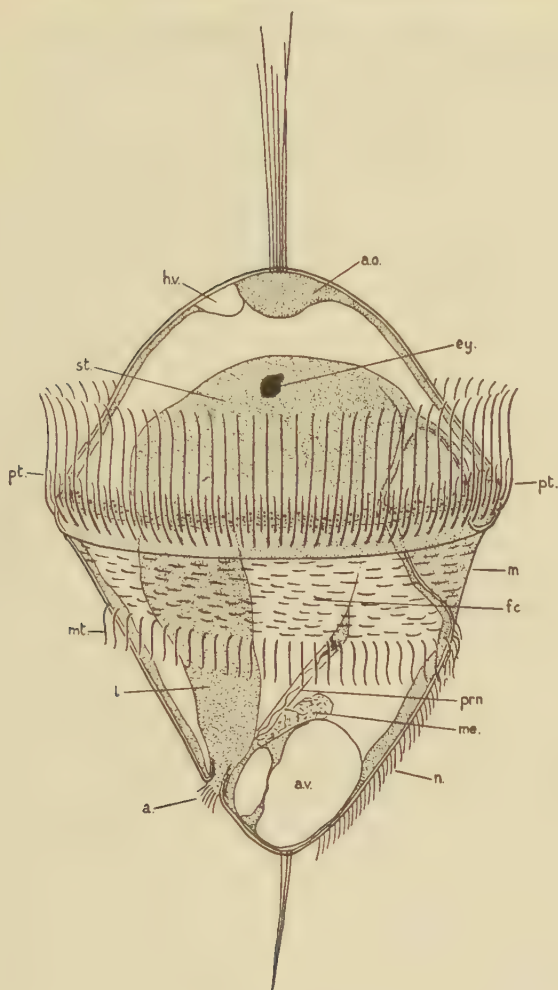
the oesophageal region by two or three tapering cytoplasmic processes.¹



TEXT-FIG. 54.

Hydroides uncinatus (Eupomatos). Diagram of early trochophore before formation of coelomesoblastic bands. *an*, anus; *anv*, anal vesicle; *coem*, coelomesoblast; *hk*, 'head-kidney'; *m*, mouth; *mesc.*, ectomesoblastic mesenchyme; *stmc*, stomach (Shearer, 1911).

¹ Shearer informed me that in *Pomatoceros* the larval protonephridium develops in the same way from ectomesoblastic nephridio-blasts which have nothing to do in origin with the coelomesoblastic teloblasts.



TEXT-FIG. 55.

Pomatoceros triqueter. Right view of trochophore showing larval protonephridium, *prn*, and small coelomesoblastic band *me* (Segrove, 1941).

According to Shearer (see above) the larval protonephridia open at first into the proctodaeum; but Segrove (1941) finds that in *Pomatoceros* (Text-fig. 55) the nephridiopores are

at first near the anus, and later are carried relatively farther forward near the collar as the trunk develops.

These larval protonephridia disappear later and are not known ever to persist in the adult.

From these various observations, incomplete as they are, we see that there is good reason for believing that the nephridia of the adult like those of the larva originate from ectodermal or ectomesodermal cells. Only coelomoducts, whether attached to or separate from the nephridia, come from coelomic epithelium.

Class Archiannelida.

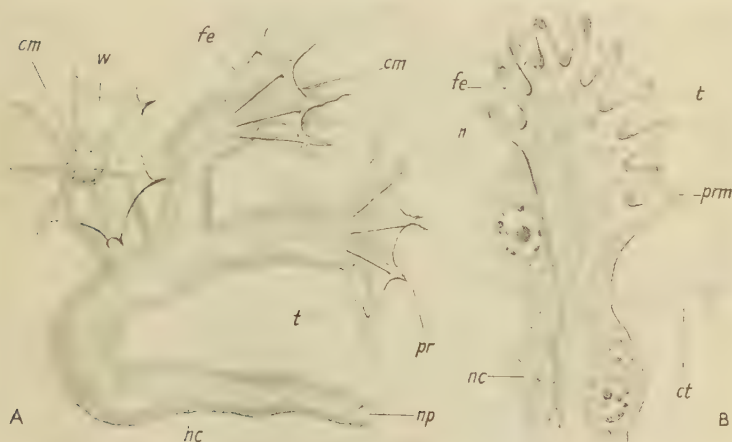
The Archiannelida are difficult to deal with. The Order comprises six Families of diverse structure, and it is by no means certain that they form a single monophyletic group. How far they are truly primitive is a debatable point; at all events, in the partial or complete loss of chaetae in many species they appear to be degenerate. The families seem to fall into divisions as follows (Goodrich, 1901, 1912, 1931).

Division 1: Polygordiidae—Polygordius, Chaetogordius. Division 2: Protodrilidae—Protodrilus; Saccocirridae—Saccocirrus. Division 3: Nerillidae—Nerilla, Nerillidium, Troglochaetus. Division 4: Dinophilidae—Dinophilus, Trilobodrilus, Diurodrilus; Histriobdellidae—Histriobdella, Stratiodrillus.

The families in Division 4 are provided with protonephridia arranged in pairs in each of the somewhat ill-defined segments of the trunk (Harmer, 1880; Korschelt, 1882; Repiachoff, 1886; Ed. Meyer, 1887; Schimkewitsch, 1895). They appear to be absent, however, in the male in the segment containing the genital ducts. It is important to note that, so far as known, these excretory organs are always of the protonephridial type. Internally the slender canal ends blindly in some sort of flame-cell situated in a space (probably not coelomic) in a segment anterior to the one on which is the external pore.

The detailed structure of the end-cell in *Dinophilus taeniatatus* has been elucidated by Shearer (1906), who found it to be a single solenocyte of complex structure, with one large

nucleus but many projecting blind tubules each bearing one internal flagellum (Text-fig. 56). This discovery was confirmed by me and figured in detail (Goodrich, 1909). The peculiar end-cell recalls the solenocytes of the *Acanthocephala* (p. 337), and even the flame-cell with many flames described by Hein in



TEXT-FIG. 56.

A, First larval protonephridium of *Polygordius neapolitanus*.

B, Inner end of protonephridium of *Dinophilus taeniatatus*.

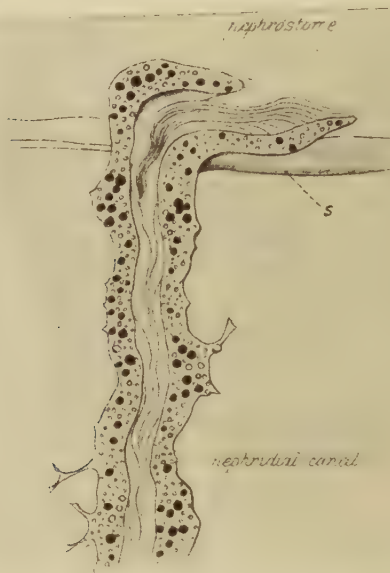
Diagrammatic from living and stained material. *cm*, central mass with single nucleus; *fe*, flagellum; *nc*, protonephridial canal; *np*, nephridiopore; *pr*, cytoplasmic process; *t*, solenocyte tube; *w*, thin cytoplasmic web (Goodrich, 1909).

the Cestode *Amphilina* (p. 134); but more especially the end-cells of the larval *Polygordius*. In *Histriobdella* the end-cell is simpler, being merely provided with an internal bunch of cilia (Shearer, 1910).

In the other Divisions the nephridia in the adult have an open funnel. This nephridiostome in *Polygordius* (Goodrich, 1900) with its distinct 'flame' of cilia is shown in Text-fig. 57. It closely resembles that of certain small Polychaetes such as the Syllidae (p. 178) and the organ appears to be undoubtedly a true metanephridium. Never have I found the wide flattened funnel described by Fraipont (1889). It should

be mentioned that the anterior end of the nephridium of the first pair, passing through the first septum, has a simple blind extremity (Text-fig. 62).

Whereas in *Polygordius* the nephridia are simple straight canals running along the inner face of the body-wall below the

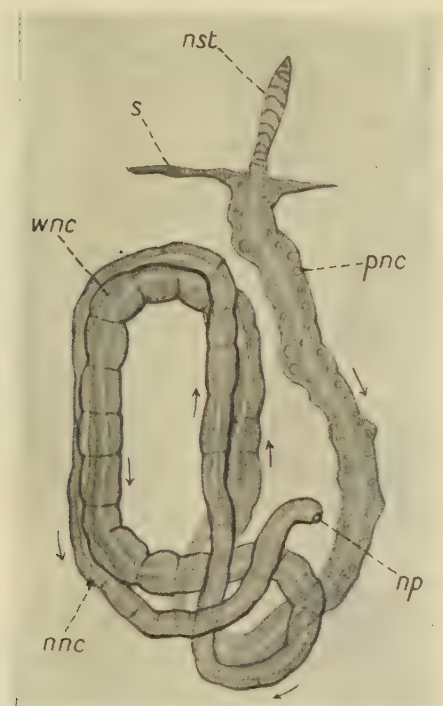


TEXT-FIG. 57.

Polygordius neapolitanus. Nephridiostome in optical enlarged section, from the living; s, septum (Goodrich, 1900).

attachment of the oblique muscles, and then bending sharply outwards to reach the external pore, in the Protodrilidae, as shown by Salensky (1907) and Pierantoni (1908), they may be considerably coiled, and project freely into the coelom with a covering of coelomic epithelium. Indeed, in the large species *Protodrilus flavocapitatus* (Text-fig. 58), the canal is so much developed and the nephridiostome so prominent, that the nephridia resemble remarkably those of the smaller Oligochaeta (Goodrich, 1931). There seems no reason to doubt that these organs (called 'macronephridia' by Pierantoni) are true

metanephridia.¹ They occur only in certain species (such as *Protodrilus spongoides*, *oculifer*, *flavocapitatus*, and also *Leuckarti*, if Hatschek's original description

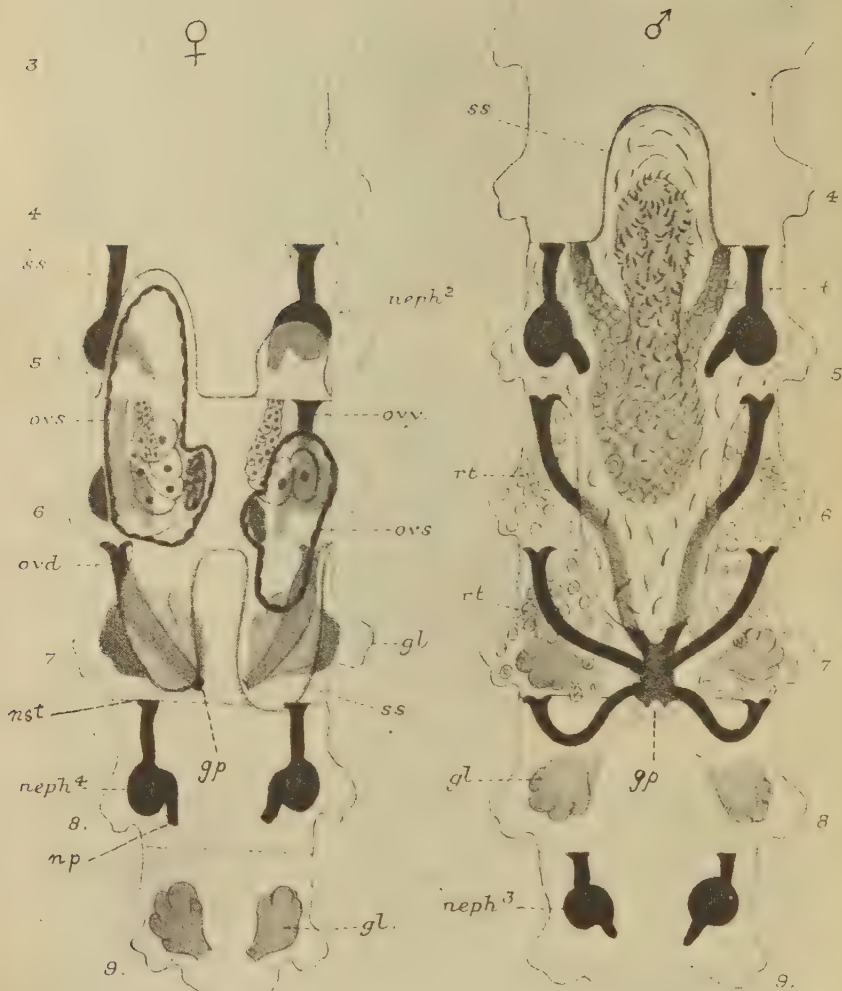


TEXT-FIG. 58.

Protodrilus flavocapitatus. Metanephridium enlarged. *nnc*, narrow canal; *np*, nephridiopore; *nst*, nephridiostome; *pnc*, postseptal canal; *s*, septum; *wnc*, wide canal (Goodrich, 1931).

is correct (1880)). But it has been shown by Pierantoni (1908) that the excretory organs in certain other species are in the

¹ The mouth of the funnel in this species appears to be crossed by cytoplasmic bars to which the cilia of the internal flame are attached, and it is not impossible that the openings between the bars are in reality closed by a thin cytoplasmic membrane (Goodrich, 1931). If this is the case, they may still be protonephridia in this species.



TEXT-FIG. 59.

form of 'brachynephridia', with a relatively short canal containing an intercellular lumen, and expanding into a widely open funnel spreading over the anterior face of the septum and the adjacent body-wall (Text-fig. 61).

The Nerillidae and Saccocirridae have similar excretory organs. In *Nerilla antennata* (Goodrich, 1912) they are restricted in the adult to segments 2, 5, 6, and 8 in the female, and segments 2, 5, 9 in the male (Text-fig. 59). The small funnel opening through the septum does not project, and its lip merges evenly into the surrounding coelomic epithelium. A 'flame' of cilia passes inwards, and a few are present in the canal which is coiled before reaching the pore. Its syncytial wall contains many nuclei and specially large excretory vacuoles. 'Nephridia' (Text-fig. 60), in all essentials the same but not coiled, occur in all segments from the third backwards (except in the sexual mid-region of the body) in *Saccocirrus* (Goodrich, 1901).

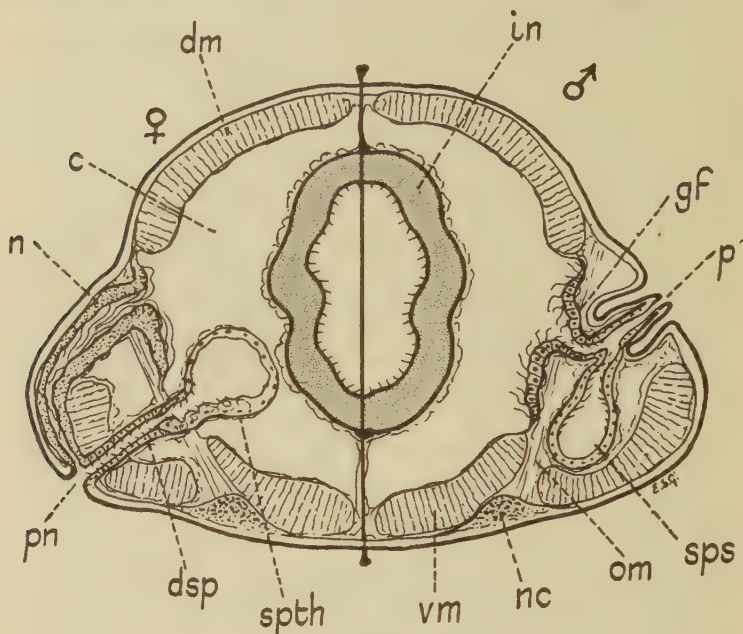
To determine the real nature of these various excretory organs of the Archiannelida it is necessary to consider their genital ducts.

In both Dinophilidae and Histriobdellidae the mature males and females have reproductive organs built on the same plan. The male *Dinophilus* has a large 'testis', extending on each side from the fifth to the first segment in paired lobes united posteriorly below the gut. It is really a testis-sac, lined by a definite epithelium from which the true testis develops in each lobe, and no doubt represents the coelom of the fifth and perhaps other segments (Harmer; Goodrich, 1895; Schimke-witsch, 1895). The whole sac is originally of paired origin in the young (Harmer in *Dinophilus*, 1889-90). The female is provided with a similar ovarian-sac. In the Histriobdellids both sexes have paired genital ducts (Haswell, 1900; Shearer,

TEXT-FIG. 59.

Nerilla antennata. Diagrams of dorsal view of male and female showing genital organs, &c. The pores are ventral. 5-8 segments; *gl*, gland; *gp*, genital pore; *neph*²⁻⁴, nephridia; *neph*² is in segment 5; *np*, nephridiopore; *nst*, nephridiostome; *ovd*, oviduct; *ovs*, ovisac; *ovy*, ovary; *rt*, modified testis; *ss*, septal sac; *t*, testis (Goodrich, 1912).

1910). The oviduct has a ciliated funnel arising from the posterior wall of the genital sac, and duct passing to a lateral pore and provided with a gland and a spermathecal diverti-



TEXT-FIG. 60.

Saccocirrus papillocercus. Diagram showing genital ducts and nephridia in transverse section of mid-trunk segment, female on left, male on right. *c*, coelom; *dm*, dorsal muscles; *dsp*, duct of spermatheca; *gf*, genital funnel (= coelomostome?); *in*, intestine; *n*, nephridium; *nc*, ventral longitudinal nerve-cord; *om*, oblique muscles; *p*, nephridiopore at end of penis; *pn*, common pore of nephridium and spermatheca; *sps*, sperm-sac; *spth*, spermatheca; *vm*, ventral muscles.

culum. The two sperm-ducts, consisting also of ciliated funnels, vasa deferentia with glands, and seminal vesicles, join to a median ductus ejaculatorius opening at the extremity of a protrusible penis developed on the anterior wall of a median genital atrium (compare *Saccocirrus*).

Essentially similar is the genital apparatus of the male

Dinophilus, the funnels being large and conspicuous; but in the female the ducts seem to have disappeared in many species, and the ripe ova emerge through a temporary median ventral pore (van Beneden, Korschelt, Harmer, 1889; Shearer, 1906). Schimkewitsch (1895), however, has described a pair of simple funnel-like oviducts in *Dinophilus vorticoides*.

These genital ducts, of the Archiannelida provided with protonephridia in other segments of the body, have generally been called 'modified nephridia'; but it is doubtful whether they comprise any nephridial element at all, and are not merely coelomoducts performing their original function. That the funnels are the coelomostomes of the genital segment there can be no reasonable doubt. Whether the whole tube (excepting the atrium probably formed from an epidermal invagination) is partly coelomoduct and partly nephridium, whether it is a nephromixium (like, for instance, that of the Phyllodocidae, where the coelomostome is grafted on to the protonephridial canal) could only be determined by following the development.

Passing now to the Archiannelida with open metanephridia, the female *Nerilla* (Goodrich, 1912) has a pair of simple oviducts, opening to the exterior by separate ventral pores surrounded by glands on segment 7, and internally by funnels on septum 6/7, the ovaries being in segment 6. The male *Nerilla* has testes in segments 5, 6, and 7, and three corresponding pairs of sperm-ducts leading to a shallow median atrium opening ventrally between segments 7 and 8. In both sexes the genital funnels of richly ciliated epithelium resemble a coelomostome, especially the sperm-funnel which projects well into the coelom. The more posterior (distal) region of the duct, on the contrary, closely resembles the canal of a nephridium. No ordinary nephridia occur in these genital segments (Text-fig. 59).

Saccocirrus has a pair of gonads and genital ducts in every segment of the extensive middle region of the body (Text-fig. 60), where there are no ordinary nephridia (Goodrich, 1901).¹ In the female the oviduct on each side joins the duct of

¹ Hempelmann (1912) described in the genital segments of the female *Saccocirrus* a second pair of ducts, in the form of tubes opening from

the spermatheca to open ventrally to the exterior (the spermatheca is probably derived from an invagination of the epidermis); while, in the male, the sperm-duct joins the seminal vesicle to open by a common duct at the extremity of a latero-dorsal protrusible penis (doubtless of epidermal origin). In *Saccocirrus* also the canal of the genital ducts closely resembles the canal of the excretory nephridia, in the sterile segments, especially in the female. On the other hand, especially in the male, the wide funnel spreads out on the anterior face of the next segment like a typical coelomostome. Here, then, there seems to be some evidence that the genital ducts are compound organs like the mixonephridia of certain Polychaetes; but no certainty can be reached on this point without a knowledge of their development.

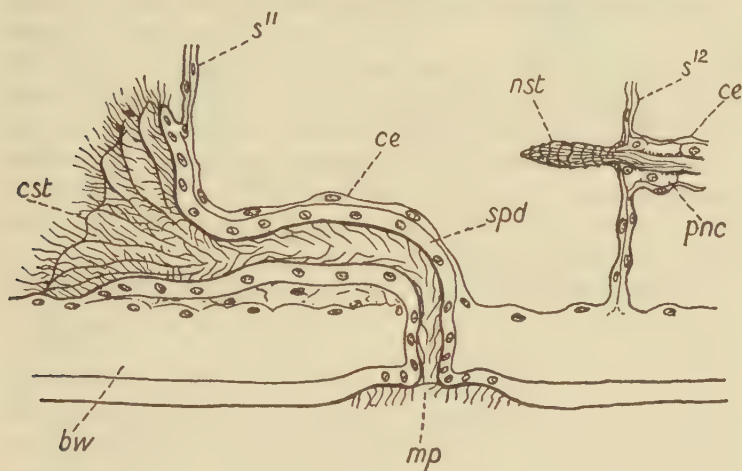
An examination of the Protodrilids reveals a somewhat different and remarkable state of things. No special ducts have been found in the female of any species of *Protodrilus*. The ripe ova appear to be always shed by the dropping off and breaking up of the posterior region of the body. Consequently no ducts are needed, and the coelomoducts have disappeared. The ciliated epithelium seen on the anterior face of the septa of the fertile segments in the female *Protodrilus flavocapitatus* may represent a vestige of the degenerate coelomostomes (Goodrich, 1931).

Genital ducts are, however, found in the fertile segments of the male sex. In those species with 'meganephridia' (metanephridia) there are sperm-ducts, for instance, *Protodrilus flavocapitatus*, with one pair of sperm-ducts in segment 13 (Text-fig. 61), and *Protodrilus oculifer* with three or four pairs in segments from the eighth backwards. It has been shown (Goodrich, 1931) that in *Protodrilus flavocapitatus* the sperm-funnel with its richly ciliated epithelium and sharp ridges presents the typical structure so often seen in the coelomostomes of Polychaeta. Doubtless these ducts represent

the spermathecae into the coelom by ciliated funnels. But I failed to find these in my own specimens, and also in the sections Dr. Hempelmann kindly sent to me for study. Since he appears to have now abandoned his first interpretation nothing further need be said on the subject.

the coelomoducts which have been preserved in the fertile segments but lost in the sterile segments.

The species of *Protodrilus* with 'brachynephridia' differ from the former in an instructive manner (Pierantoni, 1908). For in the male sex of these species the funnels of the 'brachy-



TEXT-FIG. 61.

Protodrilus flavocapitatus. Diagram showing relation of sperm-duct, *spd*, and nephridiostome, *nst*, to eleventh and twelfth septa in male. *bw*, body-wall; *ce*, coelomic epithelium; *cst*, coelomostome; *mp*, genital pore; *pnc*, postseptal nephridial canal (Goodrich, 1931).

nephridia' of from three to six fertile segments undergo at maturity a marked change, becoming transformed into large prominent, strongly ciliated, more or less cup-shaped sperm-funnels. The whole process bears a striking resemblance to that undergone at maturity by the coelomostomes in such Polychaeta as the Syllidae (p. 178). Again, it must be admitted that whether the sperm-ducts of *Protodrilus* are simply coelomoducts or nephromixia similar to the mixonephridia of Polychaeta could only be decided on embryological evidence.

There remains *Polygordius*. Its nephridia have been described above (p. 216) as genuine metanephridia, and in no

species have genital ducts been found. It is true that Perrier (1875) thought that the genital products escaped by the nephridia in *Polygordius villoti*; but he gave no definite evidence for this belief. Fraipont (1887) described the evacuation of the ova by dehiscence through the posterior region of the body, and believed the same process to occur in the male, in *Polygordius neapolitanus*. Hempelmann (1906) found this process to be accomplished in *Polygordius lacteus* by the casting off and regeneration of the posterior end. Dawydoff had previously (1905) shown that in *Polygordius epitokus* the germ-cells are gathered in the last five or six segments where the body-wall tissues degenerate. This posterior end is shed at maturity, and the anterior portion of the worm regenerates and develops new germ-cells. It may be concluded that in both sexes of *Polygordius* the coelomoduets have been lost.

Larval protonephridia.—The larval nephridia of *Polygordius* are of great interest and have attracted much attention ever since their first discovery by Metschnikoff in 1871. Hatschek in his well-known work on the development of Annelids (1878) showed that there are two pairs of larval nephridia of similar structure; the first, larger and more branched, is said to belong to the first segment of the body, the second smaller pair to the second segment. It was found by Fraipont (1887) and confirmed by E. Meyer (1901) that the inner ends of these larval nephridia do not open internally, as first supposed by Hatschek, but end blindly in special 'end-cells'. They are protonephridia.¹ This fact, that in the develop-

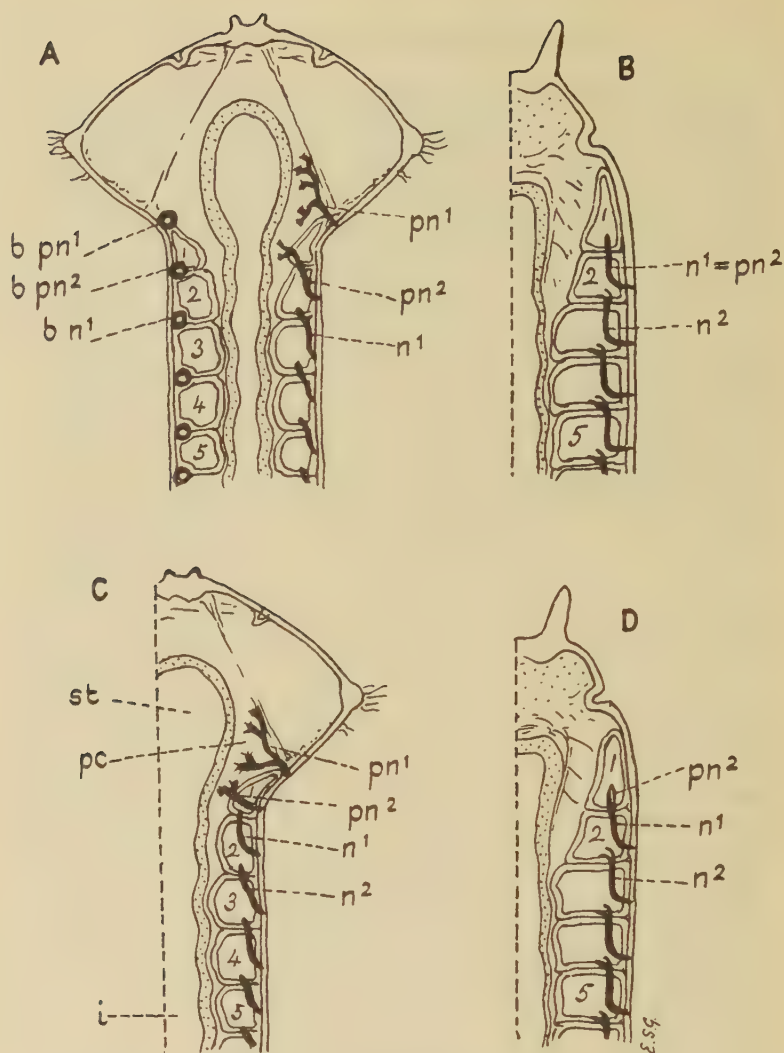
¹ Hatschek (1879) described the canal as ending in an open funnel with a thin membrane supported by radiating rodlets like the ribs of an umbrella. Fraipont and E. Meyer concluded that in the Neapolitan species the rodlets were really hollow blind prolongations of the nephridial lumen projecting from a central chamber closed by a wall containing a large nucleus. Subsequently (Goodrich, 1900), it was shown that the prolongations radiating round the central nucleus are stiff solenocyte tubes, each containing a long flagellum which extends into the chamber and lumen of the canal. The delicate membrane is supported by cytoplasmic thickenings extending to the free blind extremity of each tube (Text-fig. 56 A). Thus

ing *Polygordius* there is an uninterrupted series of segmentally disposed nephridia beginning with two pairs of protonephridia followed by open metanephridia belonging to the third and succeeding segments, was used by me (1895) as a conclusive argument for considering all so-called 'head-kidneys' projecting into the larval pseudo-coelic 'head-cavity' as merely the first pair of the segmental series of nephridia; this pair being precociously developed and enlarged for larval purposes. Such protonephridia and metanephridia would, therefore, be serially homologous organs.¹ This important conclusion has been strongly confirmed by the discovery that in many *Polychaeta* (*Phyllodoceidae*, &c.) protonephridia occur in every segment throughout the trunk.

The first pair of larval protonephridia disappears in *Polygordius* at metamorphosis, as it does in other Annelids, excretion being carried out by the more posterior nephridia.

The fate of the second pair of protonephridia in *Polygordius* is still uncertain. Hatschek (1878) believed that these protonephridia became converted into the first pair of nephridia of the adult, having lost their solenocytes; and it is now generally held that they end blindly in the first trunk segment and open to the exterior on the second. The next the single nucleus seems to control a number of separate solenocyte tubes and flagella (varying from three to six), recalling the somewhat similar structure found in the protonephridia of *Dinophilus* and certain other adult worms (Text-fig. 56). This form of end-cell was first described from an unknown species found in Ceylon, but was later found to occur in *Polygordius neapolitanus* (Goodrich, 1909). However, it does not appear in the second pair of protonephridia in *Polygordius lacteus*, where according to Woltereck (1904) the tubes are not connected by membrane and there is a nucleus to each—an observation I have confirmed on a larva in Plymouth.

¹ It will be generally admitted that the expanded 'sphere' of the trochophore larva, surrounded by its prototroch, is an adaptation to free-swimming life. The space it encloses is partly filled with a jelly-like substance while a cavity filled with clear fluid remains next to the larval stomach. This latter space (so-called 'blastocoele') is of pseudocoelic and not of coelomic origin, and has been shown by Woltereck (1905) and Hempelmann (1906) to persist round the pharynx of the adult. It is in this pseudocoelic space that the whole of the first protonephridium lies, and also the solenocyte-bearing extremity of the second protonephridium, in the larva.



TEXT-FIG. 62.

Diagram of possible interpretations of relation of nephridia to segmentation in *Polygordius*. A and C, developmental; B and D, adult stages. In B first nephridium is derived from second larval protonephridium. In D first nephridium is derived from second larval protonephridium and adult nephridium of segment 2 (Woltereck and Hempelmann). bn^1 , nephridioblast of first adult nephridial canal; $bpn^{1,2}$, nephridioblasts of first and second larval protonephridia; i , intestine; $n^{1,2}$, first and second adult nephridia; $pn^{1,2}$, first and second larval protonephridia; st , larval stomach; 1-5, coelomesoblastic somites.

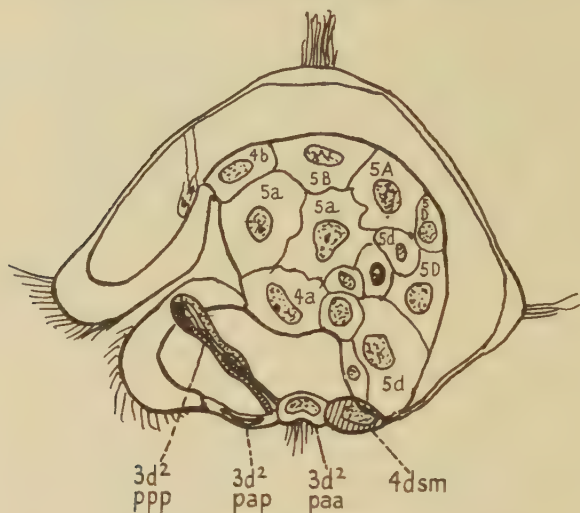
succeeding adult nephridium would then be a metanephridium with a funnel in the second and a pore on the third segment (Text-fig. 62). This view is in accordance with the results of E. Meyer (1901) as regards the order of the nephridia, and is the one I am inclined to accept, but Woltereck (1905) and Hempelmann (1906) adopt another interpretation (see also footnote on p. 229).¹

The early development of the 'head-kidney' or first larval protonephridium has been described by Woltereck (1904, 1905). Whereas during cleavage the third quartette cells in quadrants A and B are 'Urmesenchymzellen' which wander into the blastocoel, the corresponding third quartette cells in quadrants C and D are situated on either side of the oesophagus. Each passes into the 'blastocoel' and divides into anterior terminal cell and posterior canal cell attached to an epidermal cell through which the nephridiopore is later pierced ventrally (Text-fig. 63). This pair of third quartette cells may be called the first pair of nephridioblasts. Thus to Woltereck, who

¹ Woltereck (1905), however, while agreeing that the first protonephridium is anterior to the first somite, places the pore of the second protonephridium on the first segment to which this organ is said by him to belong. Both Woltereck and Hempelmann (Text-fig. 62) maintain that the adult first nephridium, with pore on second segment and blind end in first segment, is formed by the combination of the remnant of the canal of the second protonephridium with the next posterior nephridium of the series (third of the original series). Such a strange conclusion cannot be accepted without more definite evidence than has yet been given. Further investigation is needed.

Much of the confusion as to the allocation of larval and adult nephridia to particular segments may be due to the custom of describing them as 'belonging' to the segments in which lie their canals. If as maintained in this paper, the morphological position of a nephridium is really inter-segmental (as shown by the position of the nephridioblast from which it is derived), it is better described as 'belonging' to a particular septum. Thus a nephridium belonging to septum $n/n+1$ has its anterior extremity (solenocytes or nephridiostome) in segment n , and its external pore in segment $n+1$. Likewise in the case of a mixonephridium the coelomostome is in segment n , and the nephridial canal and pore are in segment $n+1$. These relations in *Polygordius* are shown in Text-fig. 62. I regret that my own observations are still too incomplete to allow me to settle the controversy.

followed the cell-lineage of *Polygordius* in detail, we owe the definite proof that these nephridioblasts pass inwards from superficial cells, grow centripetally, and have nothing to do with the coelomesoblast derived from cell $4d$; for the young first protonephridia are already formed when the two telo-



TEXT-FIG. 63.

Left-side view of trochophore larva of *Polygordius* showing protonephridium developing from third quartette cell of quadrant D. Mesoteloblast $4dsm$ of left side still undivided (Woltereck, 1903).

mesoblasts (daughter cells of $4d$), situated some distance away near the anus, are still undivided.

Shearer's observations (1907) agree on the whole with those of Woltereck and go farther (Text-fig. 89). On either side of the stomodaeum a superficial cell divides into an outer ectodermal cell and an inner ectomesodermal cell. The latter gives rise to the whole protonephridium including canal and solenocytes.¹

¹ Woltereck (1905) describes the development of the second protonephridium as follows: This organ consists of a 'mesenchymatous part' lying in the 'blastocoel' and a 'segmental part' passing through the first coelomesoblastic somite. The first part is composed of two solenocytes and one basal cell; the second part consists of an ectodermal pore-cell and

An important result of these researches is that it is clearly demonstrated that: (1) the protonephridium is of superficial ectodermal or ectomesodermal origin; (2) grows centripetally into the pseudocoelic (blastocoelic) head space; (3) the whole organ, canal as well as solenocytes, comes from one original rudiment (nephridioblast); and (4) it has nothing to do with the coelomesodermal band.

These conclusions are amply confirmed by what we know of the development of the 'head-kidneys' in other Annelida more especially from the work of Shearer (1911), see p. 211.

Class Myzostomida.

From the early work of Beard, Graff, and others it became known that the Myzostomida are provided with a pair of excretory organs which Beard recognized as of nephridial nature. They have been studied in detail by Wheeler (1896) and v. Stummer-Traunfels (1903), who has also given a useful general account of the genital and excretory organs in the whole group (1926). In most species each excretory organ is separate, and has a ciliated funnel leading from the median dorsal chamber of the coelom ('uterus') to a bent canal lined with ciliated excretory epithelium. The canal generally opens into the rectum (cloaca); but in some species, the right and left canals may join to open by a median pore to the exterior (as in *Myzostomum belli* and *Myzostomum cysticum*). Rarely the two funnels may combine also. Fedotov (1914) has described a genus, *Protomyzostomum*, with several pairs a short string of cells forming the canal and joining the basal cell. This canal resembles that of the more posterior metanephridia. The whole second protonephridium develops from a mesenchyme cell, which divides into a terminal and a basal cell (and an associated mesenchyme cell). A superficial ectodermal cell later appears which gives rise to the pore-cell and canal joining it through the somite to the basal cell. The mesenchymatous part is lost at metamorphosis, and the canal attaches itself to the anterior end of the nephridium next behind (of second segment, see Text-fig. 62). What becomes of the pore and pore-cell is not mentioned. No detailed figures of the development are given. Woltereck distinguishes emphatically between the 'mesenchymatous' and the 'segmental' parts, comparing the former to the whole first protonephridium, and the latter to the canals of the following nephridia.

of 'nephridia', usually three or four. Since their number varies and some may be incompletely developed (either funnel only or duct only) it seems probable that secondary multiplication has here taken place.

The exact homology of these excretory organs cannot at present be determined since their development is not known; but the structure of the funnel described by v. Stummer-Traunfels (1903) as of ciliated columnar epithelium passing gradually into the general epithelium of the coelom points to the conclusion that the organ is a nephromixium. Nor has the nature of the genital ducts been clearly explained.

The coelom is subdivided into separate paired branching ovarian and testicular chambers (Maidl, 1910). The testicular channels combine on either side to open by a single male pore. It is possible that the duct leading to it is a coelomoduct from the coelomic wall, the muscular copulatory organ being derived from the body-wall.

The two ovarian portions of the coelom join dorsally to form a median chamber ('uterus') into which open the funnels of the excretory organs, as already mentioned. The ova appear to escape to the exterior by a prolongation of this chamber ('oviduct') leading to a posterior pore opening into the hind-gut, or directly to the exterior behind the anus, as in *Myzostomum belli*. This female pore is probably a new formation which has supplanted in function the original paired coelomostomes of the excretory organs.

It is clear that the Myzostomida, though undoubtedly related to the Annelida, must have departed considerably from the ordinary annelidan structure, perhaps owing to their parasitic mode of life.

Class Echiurida.

The excretory organs and genital ducts of the Echiurida have long been known from the works of Spengel and others. Baltzer (1931-4) has recently given a good summary of the subject. According to him four different sets of organs can be distinguished: (1) larval protonephridia, (2) metanephridia, (3) gonoducts, (4) anal sacs.

One pair of protonephridia, originally described by Grobben and Hatschek (1880), occur in the early trochophore larva of *Echiurus* and disappear towards the end of larval life (Text-fig. 64). Each has a ciliated excretory canal with intracellular lumen opening by a ventral pore posteriorly to the prototroch.



TEXT-FIG. 64.

Larval protonephridia of A *Phoronis* (*Actinotrocha branchialis*), B *Echiurus* sp. A shows anterior end projecting beyond septum, s; B shows complete organ. Both from the living. c, outer cilia; fe, flagellum; n, nucleus; nc, protonephridial canal; pr, cytoplasmic process; t, solenocyte tube (Goodrich, 1909).

Its inner end gives off branches, which end blindly in typical solenocytes provided with a thin-walled tube containing a single long flagellum and a terminal cell-body with nucleus and slender cytoplasmic processes anchored to neighbouring structures (Goodrich, 1909). According to Baltzer (1926) and others, these protonephridia lie in the mesenchyme and non-coelomic spaces between gut and body-wall, as in other Annelids, and (contra Salensky, 1905) have no connexion with the coelomesoblast. Their first origin is not precisely known. That the canal-cells are of ectodermal origin seems probable; but that, as suggested by Baltzer (1917), the solenocytes are separately

developed from the mesenchyme is in the highest degree unlikely to be true considering what we know of the homology and development of solenocytes in general.

A pair of quite simple protonephridia occurs in the anterior parenchyma of the larval stages of both sexes of *Bonellia*, and vanish later (Baltzer, 1926).

The so-called 'metanephridia' of Baltzer (1926, 1931-4) are short ciliated canals, each with coelomic funnel and ventral pore, found in the posterior trunk region of the larval *Bonellia*: one pair in *Bonellia viridis* and two pairs in *Bonellia fuliginosa*. They remain as excretory organs in the parasitic male, but one is said to disappear in the female when the anal sacs develop.¹

The so-called gonoducts are paired tubes provided each with a large ciliated funnel open to the coelom, and a short excretory canal leading to a ventral pore. Usually the canal has a long posterior caecum projecting into the body-cavity. They appear to act as excretory organs throughout adult life, but at sexual maturity serve for the collection of the ripe genital products and their expulsion to the exterior. As a rule from one to four pairs of these organs occur anteriorly (*Echiurus*, *Thalassema*), but Ikeda (1907) has described a remarkable species, *Thalassema elegans* in which some twenty or more are distributed in groups along the trunk, and another species *Thalassema taenioides* which may have some 200 in paired bunches. In the latter species each organ has a simple tubular canal ending in a wide open funnel. That these gonoducts are not simply metanephridia can hardly be doubted; on the other hand, it is highly probable that they are nephromixia—possibly strictly homologous with the mixonephridia of *Polychaeta*.²

¹ Whether these organs are true metanephridia (according to my definition, p. 117), or nephromixia (mixonephridia like those of many *Polychaeta*), it is not possible to say at present. Baltzer, unfortunately, did not seem to realize that two kinds of funnel may open into the coelom—the nephridiostome and the coelomostome (p. 117).

² The structure and function of the funnel, and the fact recorded by Baltzer that in the ♀ *Bonellia* it develops as an outgrowth of the coelomic epithelium, may be considered as strong evidence that it is a

The 'anal sacs' are the chief permanent excretory organs, and consist of a pair of elongated contractile sacs opening posteriorly into the anal cloaca, and communicating with the coelom by a multitude of ciliated funnels (about 200 in *Echiurus* and 300 in *Bonellia*), sometimes at the end of long slender diverticula (Herdman in *Thalassema lankesteri*, 1897). The wall of the sac has an inner lining of excretory ciliated cells, a middle muscular layer, and an outer covering of coelomic epithelium continuous with the lip of the funnels.

The 'anal sac' appears early in the anal region of the trochophore larva, even before the disappearance of the protonephridia, as an urn-like sac with one funnel (the apical funnel of the full-grown sac) to which secondary funnels are added later. Its early development is incompletely known. From the observations of Hatschek (1880), Salensky (1908), and Baltzer (1917), it may be concluded that it is, at least in part, of coelomesoblastic origin. The apical funnel develops as an outgrowth of the coelomic epithelium. In spite of Baltzer's doubts it seems probable that the anal sacs are of the same nature as the gonoducts, that is either coelomoducts or nephromixia.¹

coelomostome. But there is no evidence known as yet of the presence of a distinct nephridial element in this organ. It seems, however, probable that it is a nephromixium, and also is serially homologous with the more posterior so-called 'metanephridia' mentioned above.

¹ In *Bonellia* and *Hamingia* there is marked sexual dimorphism. Only one (either the right or the left) of the single pair of gonoducts persists in the female *Bonellia*. The funnel leads into a spacious posterior chamber in which the minute males may take refuge, and an anterior chamber for the storage of ripe eggs. The opening between the two chambers is temporarily closed by a plug of mucus (Baltzer, 1926). The larva of the small highly specialized male possesses the same protonephridia and 'metanephridia' as the young female. The protonephridia disappear and the 'metanephridia' persist, but neither cloaca nor anal sacs are developed. A genital duct of complex origin and doubtful homology is formed anteriorly. Its apical pore leads into a sperm-sac, whence issues a duct provided with an open coelomic funnel. Baltzer has shown that this genital duct is not the anal sac which has shifted forwards, since both it and anal sacs coexist in certain intersexual stages. He has also given evidence that the rudiments of the mouth and stomodaeum are involved in its formation; nevertheless, his conclusion that it represents neither the 'metanephridium' nor the gonoduct of the female seems hardly justified.

Class Oligochaeta.

Already in 1895 much was known about the structure of the nephridia of the Oligochaeta from the work of Lankester (who introduced the term *nephridium*, 1877), Gegenbaur, Vejdovsky, and others. Moreover, the great diversity of structure of these organs in the higher forms had already been revealed chiefly through the researches of Beddard, Benham, and Spencer.

As a rule they are typical metanephridia¹ disposed ventrally as a pair in every segment, except the first few in the adult. Morphologically the nephridia are retroperitoneal and intersegmental in position (p. 271).

Such a good account has lately been given of the nephridia throughout the Oligochaeta by Stephenson in his monograph (1920) that it will be necessary to mention here only certain points of particular interest and some of quite recent discovery.

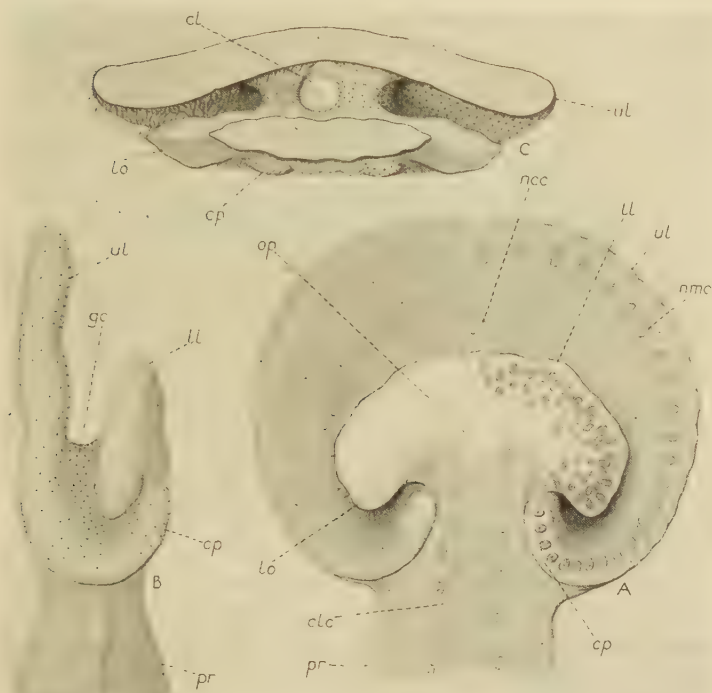
Concerning their finer structure it may be recalled that ever since Benham's classical work on the nephridium of *Lumbricus* (1891), it has been realized that, however complicated and differentiated the canal may be, it is essentially a string of cells set end to end and pierced by an intracellular lumen. Occasionally, as in the muscular vesicle (bladder) of *Lumbricus*, the canal may in the course of development acquire a wider lumen surrounded by many cells (see further, Text-fig. 75). The intracellular lumen itself may give off diverticula or even form a network of anastomosing canaliculi within the excretory canal cells (Text-figs. 66 and 67) (*Enchytraeus*, Goodrich, 1906; *Microchaeta*, Benham, 1886; *Desmogaster*, Rosa, 1890; *Moniligaster*, Bourne, 1894; *Plutellus* (= *Argilophilus*), Eisen, 1895; *Bdellodrilus*, Moore, 1897. Text-fig. 67).

The ciliation may be restricted to certain regions of the canal, where the cilia may be set round the lumen or in one or two

The funnel, at all events, has the relations and function of a coelomostome.

¹ The Naid *Chaetogaster* is remarkable in that its nephridia develop neither cilia nor funnel (Vejdovsky, 1884; Boveri-Boner, 1920); this condition seems to be secondary.

longitudinal rows. In the lower forms the cilia may form undulating 'flames' or bunches similar to those frequently found in protonephridia of *Platyhelminia* (*Enchytraeus*, Goodrich,

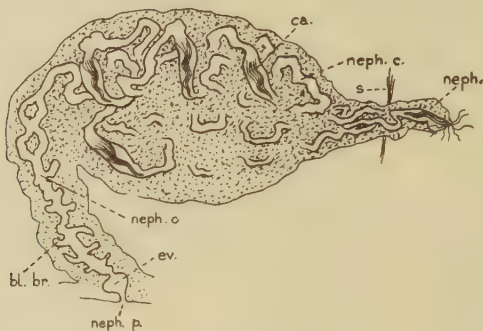


TEXT-FIG. 65.

Diagrammatic figures of nephridiostome of *Lumbricus terrestris*. A, Ventral view, cilia of upper lip, shown on right, nuclei of both lips on left. B, Right side view without cilia. C, Anterior view with lips partly cut away. *cl*, nephridial canal; *clc*, canal cells; *cp*, centripetal marginal cells; *gc*, gutter cells; *ll*, lower lip; *lo*, its lateral lobe; *ncc*, nucleus of central cell; *nmc*, nucleus of marginal cell; *op*, opening of canal into coelom, seen by transparency in A; *pr*, preseptal region; *ul*, upper lip (Goodrich, 1932).

1896, Text-fig. 66; *Rhizodrilus* (*Vermiculus*), Goodrich, 1895; *Moniligaster*, Bourne, 1894; *Bdellodrilus*, Moore, 1897).

The nephridiostome, small and simple in the lower Oligochaeta, becomes progressively larger and of more elaborate structure in the higher Lumbricids. A prominent expanded upper lip is established, consisting of many ciliated marginal cells set round a ciliated central cell first discovered by Benham (1891) in *Lumbricus*. Here the lower lip is not ciliated,



TEXT-FIG. 66.

Enchytraeus albidus. Metanephridium showing nephridiostome, *neph*, with outer selecting cilia and inner 'flame'. Similar 'flames' of cilia are seen in the canal, *ca*. *blbr*, blind branches; *ev*, end vesicle; *neph c*, nephridial canal partly hidden; *neph p*, nephridiopore (Goodrich, 1906, from Stephenson).

contains many nuclei, and usually has many amoeboid coelomic corpuscles attached to it.¹

¹ Accounts of the nephridiostomes are to be found in many papers (some of which are mentioned above), and careful descriptions have recently been given in a special work by Miss Boveri-Boner (1920) on the nephridia of the Oligochaeta. In *Stylaria* the funnel is formed of a single perforated cell with two more cells at its base forming the pre-septal canal. More nuclei occur in the funnel of *Tubifex*, but it is not until the Lumbriculids that a central cell becomes distinguished from marginals (two in *Lumbriculus*, and eight in *Rhynchelmis*). Eisen (1895) described in detail the nephridia of many genera of the higher forms, including Moniligastrids with twenty marginals, Megascolecids (*Pontodrillus*) with about twenty-four, and as many as 150 in *Megascolex dubius*. A detailed, but partly incorrect, account of the funnel in *Lumbricus* has been given by Rosen (1911), and I have myself described its structure and development (Goodrich, 1932, Text-fig. 65).

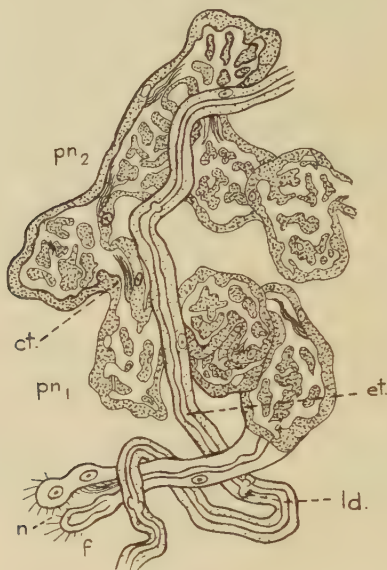
In the smaller and lower Oligochaeta ('Microdrili') delicate wavy cilia project into the coelom from the upper edge of the nephridiostome. Their function appears to be to select certain fine particles which are allowed to pass into the funnel from other particles and corpuseles which are rejected. From the inner surface of the dorsal upper lip springs the undulating 'flame' of powerful driving cilia reaching far down the lumen, particularly well shown in Enchytraeids (Text-fig. 66). It closely resembles that of a typical flame-cell, with which it is doubtless homologous. This 'flame' persists on the central cell in *Lumbriculus* and even in *Haplotaxis*, generally considered as a primitive form closely allied to the higher 'Megadrili'. The nephridiostome of *Haplotaxis* (Boveri-Boner, 1920), with its many marginals, otherwise resembles that of *Lumbricus*; but in the latter the flame has been replaced by a general ciliation.

The way in which the nephridiostome develops from the embryonic funnel-cell after it has reached its pre-septal position was admirably described by Vejdovsky (1884) in *Tubifex*, and later (1888-92) in *Rhynchelmis* (Text-fig. 74). He figures it passing from a protonephridial to a metanephridial condition (see further, p. 264).

A considerable amount of work has been done on the histology and physiology of the nephridia more especially of the higher Oligochaeta. One may mention the elaborate histological study by Maziarski (1903), and the observations of Cuénot (1898, 1902), Schneider (1896), Willem and Minne (1900), on phagocytosis and excretion of waste products (guanin, urea, cholesterin) and injected substances. More recently Cordier (1933, 1934) has carried out an experimental study on the athrocytic and phagocytic action of certain parts of the canal. As a rule delicate sifting cilia (Text-fig. 65) on the upper lip of the nephridiostome tend to prevent any but the finest particles from passing into the nephridium, and it is well known that phagocytic leucocytes accumulate on the lower lip in Lumbricids. These facts may be related to the necessity of preventing the long narrow and tortuous canal from being blocked by waste material. In the larger Oligochaeta such as Lumbricids

the large nephridia are amply supplied with blood by a network of capillaries (Benham, 1891).

An interesting condition found in *Lumbriculus* has been described by Boveri-Boner (1920). Here the much-coiled canals form longitudinal masses on either side of the ventral nerve cord,



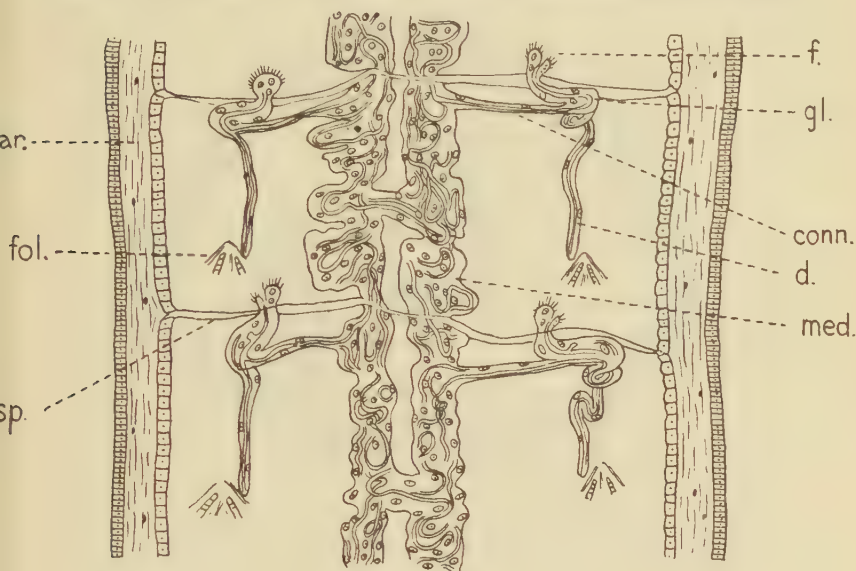
TEXT-FIG. 67.

Bdellodrilus illuminatus. Nephridiostome and part of canal showing lumen subdivided into intracellular plexus separated by connecting canals, *ct.*, with 'flames'; *et.*, efferent canal to pore (Moore, 1897, from Stephenson).

and the nephridia are said to communicate with each other not only longitudinally but also from side to side (Text-fig. 68). This condition would appear to be secondary; but the description requires confirmation.

Still more peculiar is the extensive network of anastomosing canals running in the body-wall of the Eudrilidae described by Beddard (1891, 1895). Particularly well developed in *Libyodrilus*, it there consists of four principal longitudinal trunks, two on each side of the nerve cord below the coelomic epithelium

and continuous from segment to segment, from which trunks branches arise, ramify in every direction through the longitudinal muscular layer, and finally join circular trunks running between the muscle layers completely round the body (Text-fig. 69). From the circular canals numerous ducts pass



TEXT-FIG. 68.

Lumbriculus variegatus. Metanephridial network in two successive segments. *f.*, nephridiostome; *fol.*, setal follicle; *gl.*, glandular swollen region of canal; *conn.*, connecting canal; *d.*, duct to pore; *med.*, median region with anastomosing canal; *par.*, body-wall; *sp.*, septum (Boveri-Boner, 1920, from Stephenson).

outwards to pores distributed all round. A study of young specimens led Beddard to conclude that the network has been secondarily developed from original segmental ducts to the exterior. A branching of the ducts to the exterior appears also in the Megascolecids (*Octochaetus multiporus*, Beddard, 1888; *Megascolides*, Spencer, 1888, Text-fig. 69 A).

A different type of connexion between successive nephridia has been shown to exist by Rosa (1906) in the Lumbricid *Allolobophora antipae*, where in the posterior segments,

from the thirty-sixth backwards, the nephridia instead of opening independently to the exterior join on each side to a longitudinal dorso-lateral retroperitoneal canal on the inner surface of the body-wall. These canals unite posteriorly to open by a median pore into the gut (at junction of endoderm with



TEXT-FIG. 69.

Libyodrilus, diagram of transverse section showing one meganephridium, 5, and connecting network in body-wall; 6, longitudinal trunk (Beddard, 1895).

proctodeum, five segments from anus). The persistence in one case of the usual segmental ducts leading from the longitudinal canal to the exterior shows that the latter is a new secondary formation (see also Text-fig. 72 D).

Benham (1888) made the interesting discovery that the Glossoscolecoid genus *Tritogonia* (= *Brachydrilus*) possesses two pairs of nephridia per segment (of which those of the ventral row but not of the dorsal row have funnels). But it was not until Beddard and others began the study of earthworms of the large Family Megascolecidae that the astonishing diversity of structure of the nephridial system was revealed (Beddard, 1885; Benham, 1886; Fletcher, 1886).

That the nephridia of '*Perichaeta*' were represented by

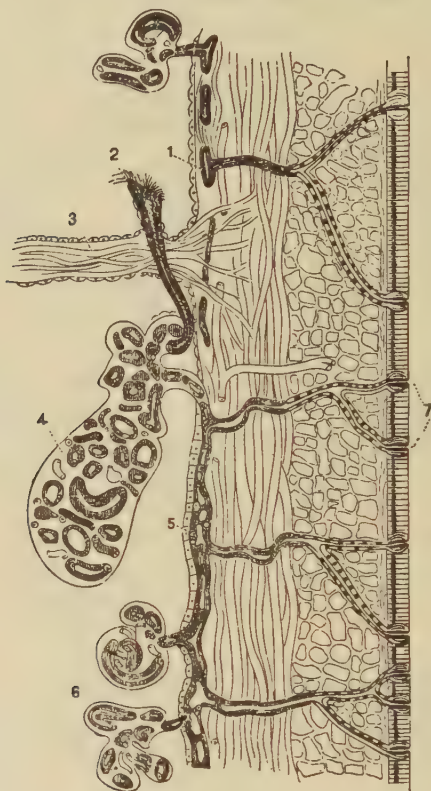
scattered tufts on the coelomic wall had been noticed by Perrier (1873), and in 1888-9 Beddard gave a detailed description of a new type of nephridial system (in *Acanthodrilus* (= *Octochaetus*) *multiplus*, and *Perichaeta* (*Pheretima*) *aspergillum*), which he called the 'diffuse' and Benham later called the 'plectonephric' system. Instead of the usual large paired organs related to the septa were here found numerous small nephridia, scattered and spread over the coelomic wall, and consisting of coiled delicate tubules opening to the exterior by corresponding ducts, and opening to the coelom by corresponding funnels in *Pheretima* and *Octochaetus*. Very numerous external pores occurred in *Octochaetus* owing to the ducts branching in the thickness of the body-wall on their way to the surface. Moreover, it was stated that a retroperitoneal network of branching intercommunicating tubules extending not only over each segment but also from segment to segment, united all the minute nephridia and so joined them into a continuous system.

At the same time Spencer (1888) gave a detailed account of the nephridia in *Megascolides australis* (Text-fig. 69A), showing that large paired funnelled nephridia were clearly distinguishable in the posterior segments; but became, so to speak, broken up more and more in the more anterior segments into numerous small nephridia until farther forward these minute nephridia without funnel alone remained spread over the body-wall. A continuous network of canals was also described uniting all the nephridia of a segment and by means of ventral longitudinal canals joining them from segment to segment. The ducts to the exterior branched in the body-wall to open on the surface by numerous scattered pores (the fate of the 'plectonephric' theory will be discussed later, p. 259).

A great variety in the number, disposition, and detailed structure of the nephridia in various genera has since been described by Bage (1910), Stephenson (1915), Cognetti (1911), Bahl, and others (see Stephenson, 1930).

It may now be explained that for convenience in descriptions three kinds of nephridia came to be distinguished in the earthworms or 'Megadrili'. These are the (1) *meganephridium*,

(2) micronephridium, and (3) 'tufted' nephridium. The first type is the ordinary paired large nephridium such as occurs in *Lumbricus* in every segment throughout the body (except



TEXT-FIG. 69 A.

Megascolides australis. Longitudinal section showing nephridial system. 1, canal; 2, nephridiostome of 4, 'meganephridium'; 3, septum; 5, connecting canals; 6, 'micronephridium'; 7, nephridiopores (Spencer, 1888, from Beddard).

the first few in the adult). Typically it is attached to a septum, with a preseptal funnel, a coiled postseptal canal in two lobes, and a third lobe containing a terminal swollen muscular bladder which empties periodically through the nephridiopore. The

second type, the micronephridium, is typically small, not related to a septum, but fixed to the body-wall, where it opens directly to the exterior without bladder. Usually it has no nephridiostome and is blind internally. Intermediate forms frequently occur.

Of less general importance is the third kind, the 'tufted' nephridium. This name is given to certain large paired organs usually restricted to a few quite anterior segments, but sometimes found in segments 3-9 (as in *Megascolex eunephrus*, Cognetti, 1911), or even throughout the body (*Megascolex filiciseta*, Stephenson, 1915). Each is composed of a bundle of nephridial lobes, usually without funnels, and all joining to a common duct. First recognized as modified nephridia by Perrier, 1873, they were found to discharge a fluid supposed to soften the food into the lumen of the pharynx and not to the exterior. Benham called such nephridia opening into the buccal cavity or pharynx 'peptonephridia',¹ but they are now generally called 'pharyngeal'; 'stomodeal' would be a better name.²

Although the terms meganephridium and micronephridium have for long been in use it was soon realized that a sound classification should be based on something more than mere size. Therefore, after it had been shown by Vejdovsky in *Megascolides* (1892), by A. G. Bourne in *Mahbenus* (1894), by Beddard in *Octochaetus* (1895), and by Bahl in *Pheretima* (1922) that the presence of more than one pair of nephridia in a segment was due to the subdivision in later development of the original paired rudiments (see p. 271), the name meronephridia was proposed by Michaelsen (1928) instead of micronephridia, and the term holonephridia may be used to emphasize the undivided character of the ordinary,

¹ The 'salivary glands' of the Enchytracidae are possibly of the same nature.

² The so-called 'anal nephridia' of the Megascolecoid *Octochaetus multiporus* may here be mentioned. According to Beddard (1888, 1895) there occurs in the posterior region of this worm a complex network of nephridial tubules provided with many funnels, and giving off in each segment several ducts to the exterior as well as several branches which open into the gut. If correctly described it would be a 'plectonephric' system both exonephric and enteronephric (see pp. 241, 260).

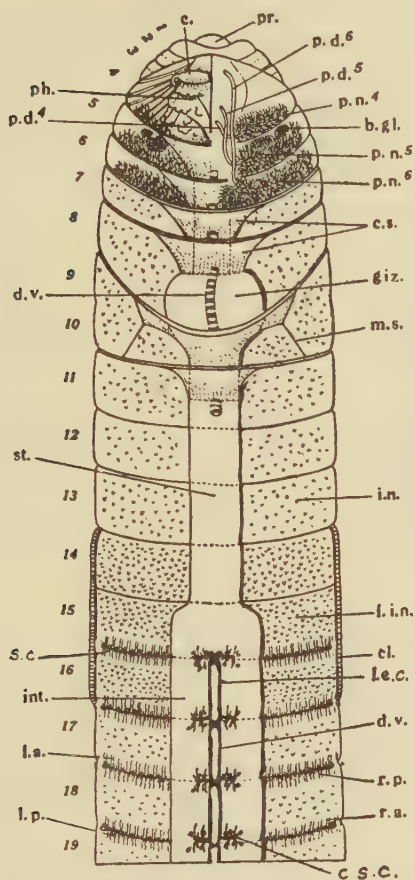
paired complete organs. Those nephridia which develop and retain a nephridiostome are said to be 'open', and those which lose or do not develop a nephridiostome are said to be 'closed'.

To the more recent and remarkable work of Bahl we owe a great advance in our knowledge and understanding of the structure, embryonic development, and physiology of the excretory system of the Megascolecidae. One of the most important results of his researches is the conclusion that there has been a progressive and divergent specialization of the meronephridia (for definition see p. 243) into two sets—one still opening to the exterior and the other opening into the lumen of the gut. Those which secrete to the exterior are called *exonephric*, and those which secrete internally are called *enteronephric* (Bahl, 1919).

As an example in which the latter system is fully developed we may take *Pheretima posthuma* (Text-fig. 70) so well described by Bahl (1919): There are three pairs of 'tufted' pharyngeal nephridia in segments 4, 5, 6. They are closed and discharge their products into the pharynx by three pairs of long ducts, and are therefore 'enteronephric'.

Separate meronephridia (*micronephridia*) are present in large number scattered over the body-wall from segment 7 backwards. They open separately to the exterior, have no funnel, and are strictly speaking *exonephric* 'integumentary' meronephridia.

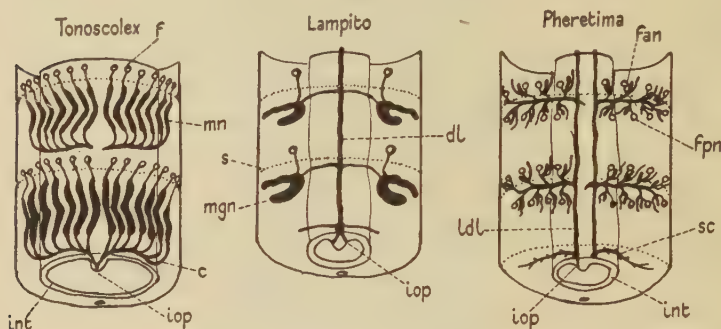
Attached to the septa in all the segments from the fifteenth backwards are 'septal' meronephridia provided with funnels. They occur right and left in rows of about forty to fifty nephridia on the anterior and on the posterior face of each septum beginning at septum 15/16. The bodies and funnels of the anterior row project into the segment in front, those of the posterior row into the segment behind. On each side all the ducts of the nephridia, anterior and posterior, join to a common 'septal canal'. The right and left septal canals run dorsally to empty into longitudinal 'supra-intestinal excretory canals' at every intersegmental interval (Text-fig. 71). These two canals run close to each other in the mid-dorsal wall of the intestine continuously from the fifteenth to the last segment. They



TEXT-FIG. 70.

Pheretima posthuma. General plan of nephridial system (see Text-fig. 71). *dv*, dorsal blood-vessel; *bg*, blood-glands; *fin*, crowded integumentary meronephridia; *giz*, gizzard; *in*, integumentary meronephridia; *la*, *lp*, left, and *ra*, *rp*, right anterior pre-septal and posterior post-septal meronephridia; *csc*, cut dorsal end of septal canal; *sc*, latero-ventral septal canals cut off from *csc* to allow spreading of body-wall; *lec*, longitudinal enteronephric excretory canals; *pd*^{1, 2, 3}, pharyngeal nephridial ducts; *ph*, pharynx; *pn*^{1, 2, 3}, tufted pharyngeal nephridia (from Bahl's figures, 1919).

communicate with each other at every septum, and are united and blind at their anterior and posterior ends. A series of intersegmental pores either to the right or the left of the base of the typhlosole are the openings (guarded by sphincter muscles) of short ducts leading from the longitudinal canals to the lumen of the intestine. Thus this whole connected system of septal nephridia is enteronephric, and their excretory products are

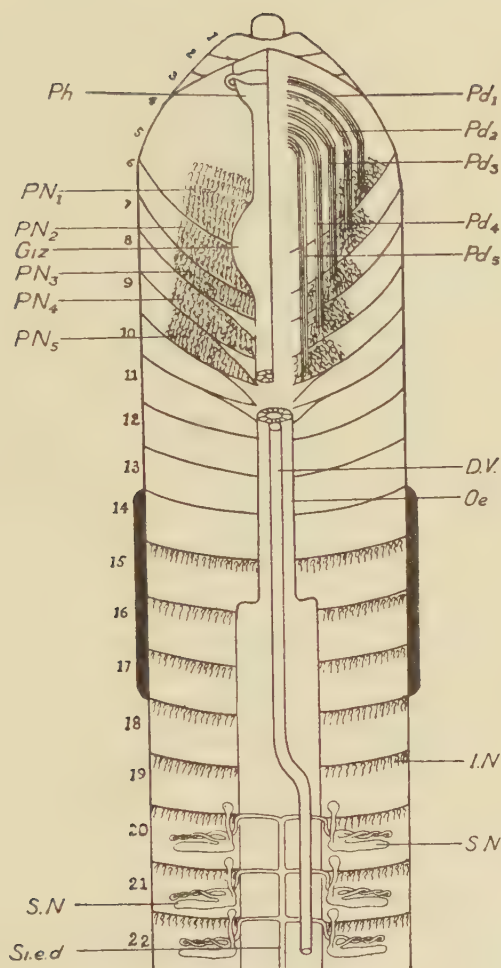


TEXT-FIG. 71.

Diagrams of enteronephric systems in *Tonoscolex*, *Lampito* (*Megascolex*) *trilobata*, and *Pheretima*. *c*, terminal canals which join on each side to terminal duct; *dl*, median dorsal longitudinal duct; *f*, nephridiostome; *fan*, *fpn*, nephridiostomes of anterior and posterior rows of septal meronephridia; *int*, intestine; *iop*, opening into intestine; *ldl*, left dorsal longitudinal duct; *mgn*, meronephridium; *mn*, septal meronephridium; *s*, position of intersegmental septum (from Bahl's figures).

poured into the endodermal gut. The nephridia themselves should, strictly speaking, be called enteronephric 'septal' meronephridia; and the whole system constitutes the intestinal enteronephric system.

In *Lampito* (*Megascolex*) *trilobata* the nephridial system is very similar to but differs from that of *Pheretima* in certain interesting ways (Bahl, 1924). For instance the enteronephric pharyngeal closed nephridia, which occur in paired masses in segments 5 to 9, have passed beyond the stage of 'tufted' nephridia with common ducts to that of independent meronephridia each with a slender duct passing forwards to



TEXT-FIG. 71 A.

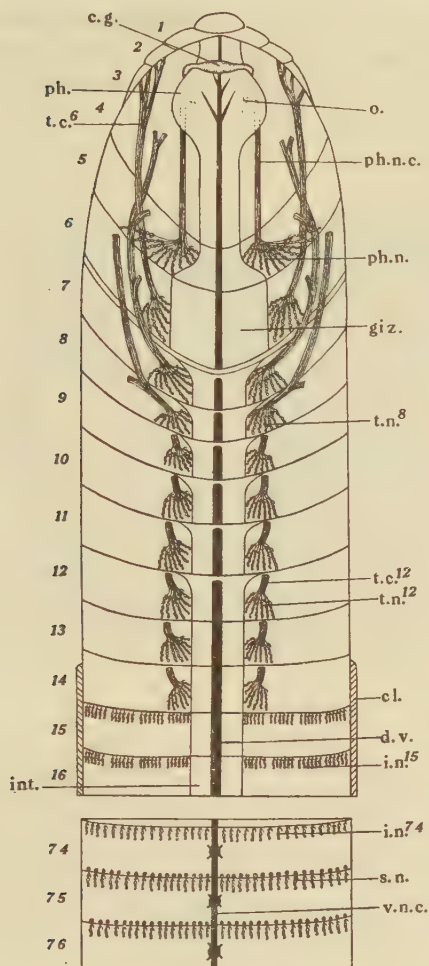
Megascolex (Lampito) trilobata (Bahl, 1924). Plan of nephridial system. *dv*, dorsal vessel; *giz*, gizzard; *in*, integumentary meronephridia; *oe*, oesophagus; *pd₁-pd₅*, sheaves of ductules of pharyngeal meronephridia opening into pharynx which has been partly cut away; *ph₁-pn₅*, segmental masses of pharyngeal meronephridia exposed by removal of their ducts; *ph*, pharynx; *sied*, supra-intestinal excretory longitudinal duct opening into intestine, and receiving transverse septal excretory canals from large paired metanephridia, *sn*.

open separately into the lumen of the pharynx (Text-fig. 71A). Minute closed exonephric integumentary meronephridia are restricted to a ring behind each septum from the fifteenth segment backwards; but the intestinal enteronephric septal system (Text-fig. 71) is represented in each segment from the twentieth backwards, by a single pair of large meronephridia (so-called meganephridia). Each has a preseptal funnel, and a long duct passing upwards to the posterior face of the septum to open into a median longitudinal supra-intestinal excretory canal running from the twentieth to the last segment. At each inter-segmental region right and left ducts lead from the longitudinal canal to the lumen of the intestine. The genus *Woodwardiella* (Bahl, 1926) has an essentially similar enteronephric intestinal system beginning at septum 24/25, and two bundles of enteronephric pharyngeal meronephridia in segment 4.

Megascolex cochinchensis (Bahl, 1942a) is remarkable in having a simpler enteronephric intestinal system without longitudinal collecting canal (Text-figs. 71, 71 B, and 71 c). Every septum, from the seventy-fourth backwards, bears on either side a series of about twenty open septal meronephridia whose terminal ducts join to form a right and a left septal canal. These canals meet in the mid-dorsal line to form a short median excretory canal which pierces the wall of the intestine and opens into its lumen. Thus every posterior segment has its own enteronephric system of septal meronephridia, resembling that of *Pheretima*, but there are no longitudinal inter-segmental connexions.

Similar segmental groups of open enteronephric septal meronephridia exist in *Tonoscolex* (Bahl, 1941), but in this genus the number of nephridia is smaller, and the septal canal less developed (Text-fig. 71).

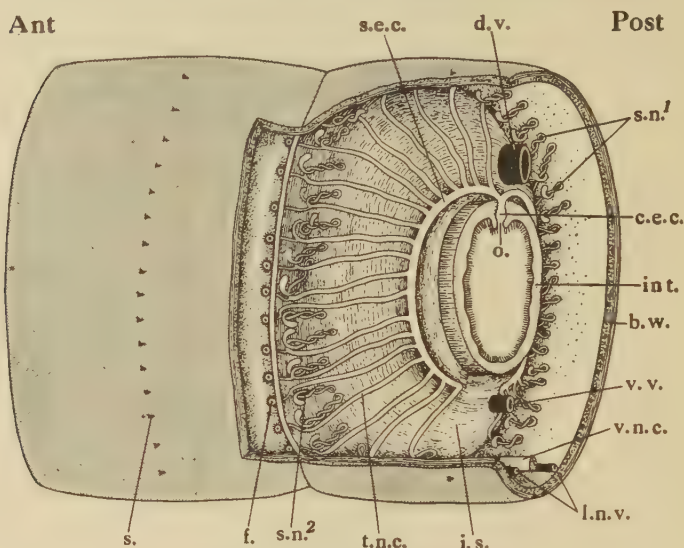
Lastly, according to Bahl (1944, in the press), *Megascolex ceylonicus* and *Megascolex sarasinorum* have what appear to be the simplest intestinal enteronephric systems so far known. The first species develops in all segments behind the thirty-second (length of worm about 190 segments) septal meronephridia with preseptal funnels. At first they are very small and only three or four in number on each side; in more



TEXT-FIG. 71 B.

Megascolex cochinensis. Plan of nephridial system, simplified (Bahl, 1942a). *cg*, cerebral ganglia; *cl*, clitellum; *dv*, dorsal vessel; *giz*, gizzard; *in*, integumentary meronephridia; *int*, intestine; *o*, concealed opening of pharyngeal duct into lumen of pharynx; *ph*; *phn*, pharyngeal meronephridia, and *phnc*, their bundles of ductules; *sn*, septal meronephridia without canals; *tc*, ductules of exonephric tufted meronephridia. Septal enteronephric canals shown in Text-fig. 71 c.

posterior segments they become larger and more numerous, until from the eighty-fifth segment backwards they are twenty on each side. A long postseptal canal passes back to the body of the meronephridium, and a long terminal duct passes for-

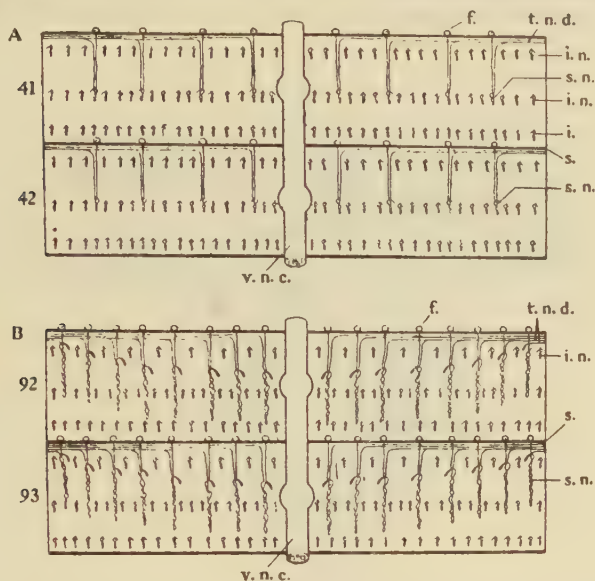


TEXT-FIG. 71 C.

Megascolex cochinensis. Diagram of enteronephric nephridial system in segments behind 74th. *b.w.*, body-wall; *cec*, common excretory canal; *dv*, dorsal vessel; *f*, funnel of septal meronephridium; *int.*, intestine; *is*, intersegmental septum; *lnv*, lateral neural vessels; *o*, intersegmental median excretory pore into intestine; *s*, seta; *sec*, septal canal; *sn*¹, *sn*², right and left septal meronephridia; *tnc*, terminal nephridial duct; *vnc*, ventral nerve-cord; *vv*, ventral vessel (Bahl, 1942 a).

ward to the septum, up which it runs dorsally to near the middle line. The septal nephridia are to a great extent attached to the inner surface of the body-wall rather than to the septum. All the terminal ducts on each side of each segment are gathered in a sheaf dorsally, and meet those of the other side in the typhlosole where they open by separate pores into a small saccule which leads by a segmental aperture into the lumen of

the intestine (Text-fig. 72 c). Behind the region of the typhlosole there are no saccules and the ducts open into the intestine by segmental groups of two or three dorsal pores on each side.



TEXT-FIG. 72 A AND B.

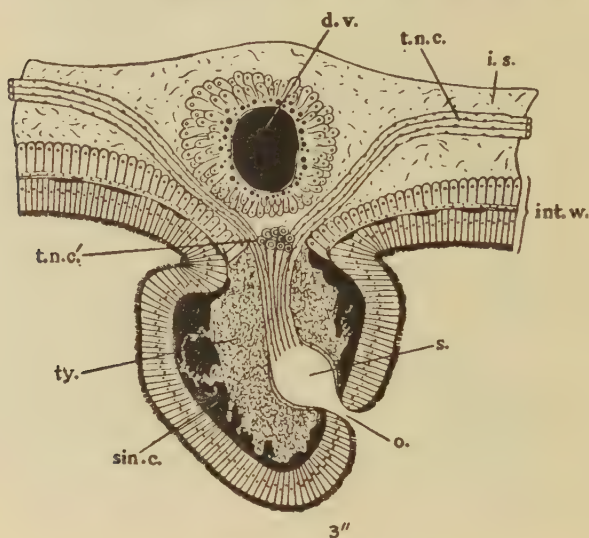
Megascolex ceylonicus (Bahl, 1944). A, The septal and integumentary nephridia in the forty-first and forty-second segments. B, The same in the ninety-second and ninety-third segments (semi-diagrammatic). *f*, funnel of septal nephridium; *in*, integumentary nephridium; *s*, intersegmental septum; *sn*, septal nephridium; *tnd*, terminal nephridial canals; *enc*, ventral nerve-cord. The actual number of septal nephridia in B should be about twenty on each side, but only eight are shown for the sake of clearness; similarly, the actual number of integumentary nephridia is much larger than is shown in A and B. (\times circa 4.)

Thus there are no septal canals and no longitudinal excretory canals.

The very small closed integumentary exonephric meronephridia extend forward into the second segment, become very numerous over the whole inner surface of the clitellar segments, but are restricted to three rows from the eighteenth segment backwards (Text-fig. 72 A and B). Pharyngeal endonephric

meronephridia occur in paired groups in segments 2-5, and their terminal canals pass forward in sheaves to open separately into the buccal and pharyngeal cavities.

The nephridia of *Megascolex sarasinorum* are almost



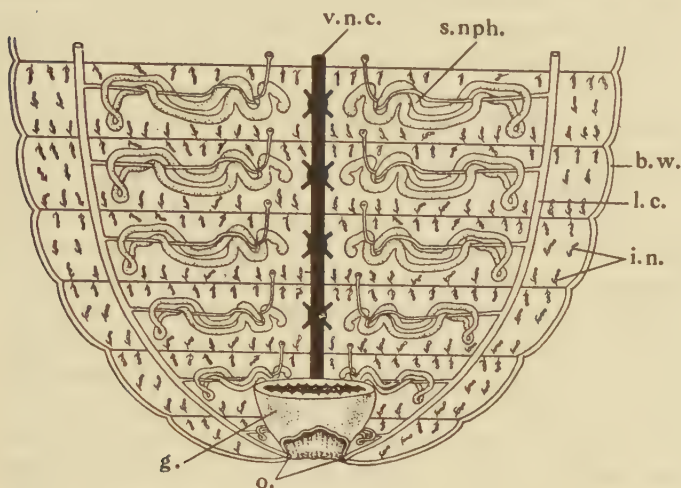
TEXT-FIG. 72 C.

A reconstruction from a few consecutive sections passing through the typhlosolar region of the intestine of *Megascolex ceylonicus* (Bahl, 1944) showing sheaves of terminal nephridial canals of the right and left sides entering the typhlosole and uniting to form a saccule just before opening into the intestinal lumen by a single opening. *dv*, dorsal vessel; *intw*, wall of the intestine; *is*, intersegmental septum; *o*, opening of the saccule into the lumen of the intestine; *s*, saccule formed by the union of the terminal nephridial canals; *sinc*, sinusoid capillaries; *tnc*, three terminal canals of the sheaf; actually there are 15 to 20; *tnc*, a group of terminal nephridial canals cut in section; *ty*, typhlosole. (\times circa 66.)

exactly the same, except that the intestinal enteronephric system is even simpler. The open septal meronephridia, which begin at segment 80, are attached to the septa (as in *Pheretima*) and not at all to the body-wall, and their terminal ducts run up in a sheaf on each side on the posterior face of the

septum towards the mid-dorsal line where they come to open separately into the intestine. No septal canal, no longitudinal dorsal canal, not even a saccule is formed.

It may be said that the various genera of Megascolecids



TEXT-FIG. 72 D.

Hoplochaetella bifoveata. Semi-diagrammatic drawing of nephridial system in last six segments. Dorsal view. *bw*, body-wall cut open and spread out; *g*, hind end of gut almost entirely removed; *in*, small integumentary meronephridia; *lc*, longitudinal lateral excretory canal opening to exterior at *o*; *snph*, large open septal nephridium opening into lateral canal; *vnc*, ventral nerve cord (Bahl, 1942).

described above doubtless represent more and more primitive stages of the intestinal enteronephric system, but they are not necessarily consecutive phylogenetic stages in the specialization of these very labile meronephridia.

In the Subfamily Octochaetinae of the Family Megascolecidae some genera, like *Eutyphoeus* (Bahl, 1942), have pharyngeal, septal, and integumentary meronephridia; but there is no intestinal enteronephric system at all, the septal meronephridia occurring in the posterior region as a pair of large open sac-like exonephric organs in each segment in addition to the usual

exonephric integumentary meronephridia. The pharyngeal meronephridia are closed and enteronephric as usual. The genus *Hoplochaetella*, however, has a quite peculiar system in the intestinal region (Bahl, 1942). For here in every posterior segment there is a pair of large open meronephridia, which discharge on either side into a dorsal longitudinal connecting canal on the inner surface of the body-wall (Text-fig. 72 D). These two canals open on each side of the anus exonephrically. This arrangement closely resembles that described by Rosa in the Lumbricid *Allolobophora antipae* (1906); where, however, the longitudinal canals join and open into the intestine by a median dorsal pore (see p. 239), and the system appears to be enteronephric. In spite of resemblance, the system in *Hoplochaetella* has probably developed independently of that in the Lumbricid.

The Function of the Intestinal Enteronephric System.—From the above account it may be concluded that in the Megascolecidae the nephridia become differentiated into three kinds: pharyngeal, integumentary, septal. The 'integumentary' are always meronephridial, and usually minute, closed, scattered, and excrete directly to the exterior; they are, therefore, exonephric. The 'pharyngeal' (stomodeal) are the most anterior, may be either 'tufted' or meronephridial, are generally closed internally and open into the buccal cavity and pharynx. The 'septal' are meronephridial, open, usually large. They are related to the septa in all the posterior segments, and extend forwards to near the clitellar region, rarely into it, but never in front of the clitellum. This septal system is the most interesting of the three kinds for, as discovered by Bahl, in such genera as *Pheretima*, *Lampito*, *Woodwardiella*, *Megascolex*, and *Tonoscolex* the whole septal system excretes not to the exterior but into the lumen of the endodermal gut. It may be distinguished as the intestinal enteronephric system, and with it may be associated the pharyngeal nephridia also enteronephric.

This intestinal enteronephric system is of special interest since Bahl (1934) has been able to offer an explanation of its

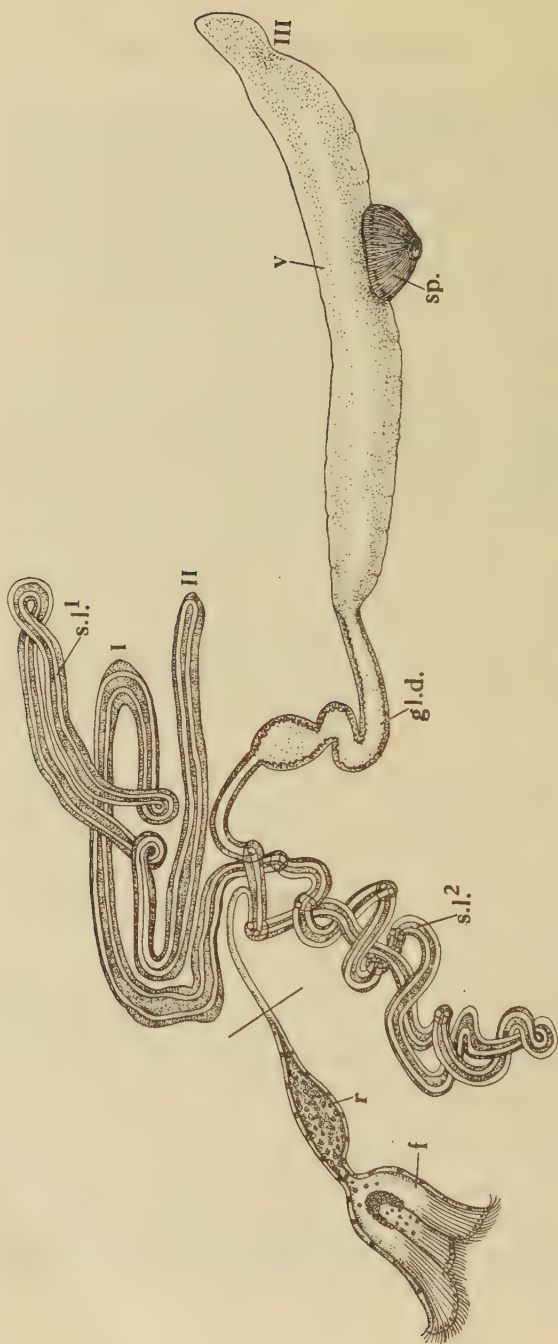
adaptive significance supported by ample evidence. Under the special conditions in which these worms live in a hot and dry climate, he maintains that it is a great advantage to them to be able to conserve much of their water which is to a great extent returned to and reabsorbed by the intestine. Rarely has so convincing a demonstration of the physiological meaning of a specialization in the structure of nephridia been given.

The Relation of the Meronephridial to the Holonephridial Condition.—There can be little doubt that the condition with many nephridia per segment has been secondarily derived from an original distribution of only one pair of metanephridia in every segment as in other Oligochaeta. This is the view now generally held. Probably a multiplication of nephridia has taken place in various families and genera independently, and perhaps not always in exactly the same way. But it may at once be stated that multiplication is by growth, some sort of budding, and subdivision of the primary paired nephridia either in embryonic or in later stages. Such secondary derived nephridia are now called meronephridia, as mentioned on p. 243.

In the case of the tufted nephridium it has been clearly shown by Bahl that it merely represents an intermediate stage between the original holonephridium and the group of completely separated meronephridia.

It should be noted that the bladder (vesicle) disappears as such in the process of differentiation and subdivision of the terminal ducts whether exonephric or endonephric.

In the Glossoscolecoid *Pontoscolex corethrurus* (Bahl, 1942*a*), where the large paired holonephridia of the post-clitellar segments have the usual three main lobes and in addition a small supplementary loop of the twisted region of the canal, the transition can be traced (Text-fig. 73). Successive new supplementary loops are added in the more anterior pre-clitellar segments, and each of these loops develops into the body of a two-lobed meronephridium, incomplete in that the funnel is absent and the terminal duct still opens into the single original common duct. This duct represents the narrowed and



TEXT-FIG. 73.

Pontoscolex corethrurus (Bahl, 1942). Nephridium from a clitellar segment (\times circa 86). *f*, funnel; *gld*, glandular duct; *sl*^{1,2}, first and second supplementary lobes; *r*, receptacle; *sp*, sphincter around the nephridiopore; *v*, vesicle (bladder); *I*, *II*, *III*, three main lobes.

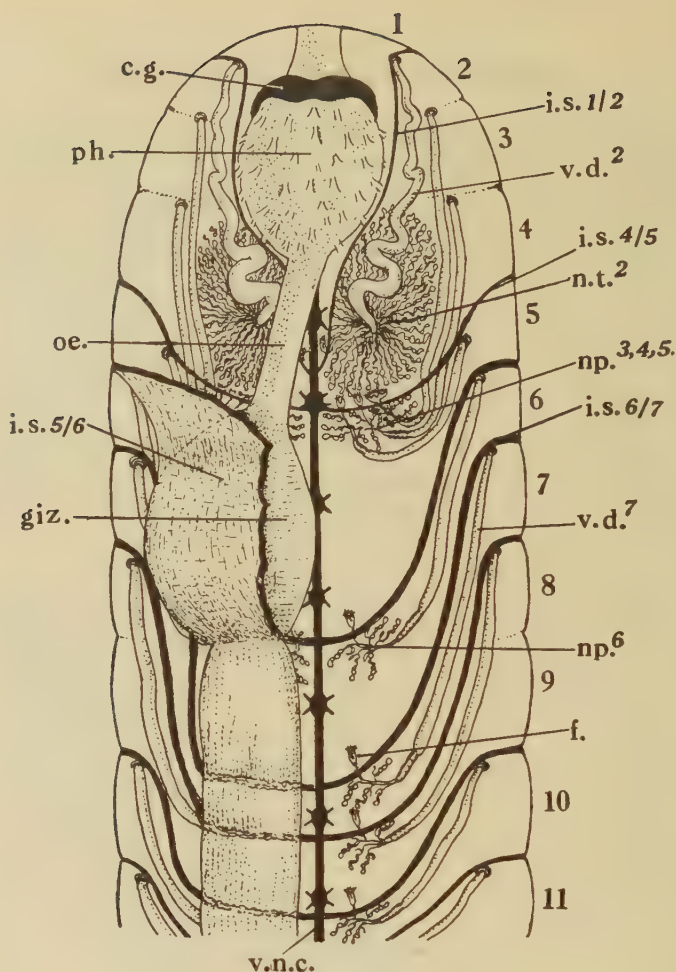
lengthened third or bladder lobe leading to the exonephric pore. The most anterior pair of the series (Text-fig. 73 A) belonging to septum 1/2, forms two conspicuous tufts each of some 100 meronephridial outgrowing loops joining the duct which opens near the mouth (see Text-fig. 73 A). In every segment the original pair of preseptal funnels persists, even the first.

Megascolex cochiniensis is somewhat similar (Bahl, 1942 a). Here the nephridia of the anterior fourteen segments are paired bunches of closed meronephridia (Text-fig. 71 B). The funnels have been lost, and the excretory ducts split into separate ductules. These open independently to the exterior, except the ductules of the most anterior and largest bunches (lodged in segment 5) which open into the pharynx¹ (see also *Megascolex trilobata*, p. 246, Text-fig. 71 A).

Observations on the development of the exonephric micro-nephridial system strongly support the conclusion that it is secondary (Text-fig. 73 B). As first shown by Vejdovsky (1892) in late embryos of *Megascolides australis* the 'meganephridia' first develop from independent paired rudiments (which acquire preseptal funnel, postseptal 'neck', dorsal loop, and external duct), the 'micronephridia' arise as a series of loops budded off from the elongated postseptal 'neck' region of the first rudiments. These secondary loops become separated off, and each acquires a duct to the exterior but no funnel. Bourne (1894) confirmed and extended these observations on *Mah-benus imperatrix*, showing how tertiary and succeeding generations of 'micronephridia' may again be budded off from the 'neck' of the 'micronephridia' until 100 or more may be formed in the same segment. The original nephridiostome here degenerates.

Bahl (1942 a) has recently further confirmed these conclusions by observations on the late embryo of *Eutyphoeus* where, in the trunk segments behind the ninety-seventh, the paired

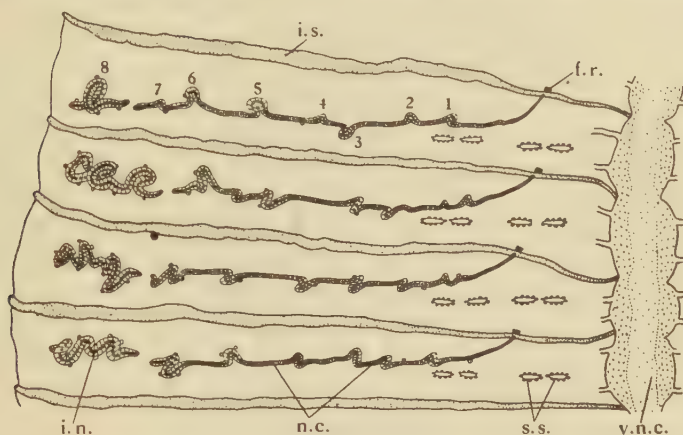
¹ The paired groups of funnelled nephridia detected by Stephenson (1930) in the trunk segments of *Megascolex (Lampito) dubius* have been shown by Bahl (1926) to belong to clusters of five small separate meronephridia obviously the result of the subdivision of paired nephridia, and probably representing 'septal' exonephric meronephridia.



TEXT-FIG. 73 A.

Pontoscolex corethrurus. The general plan of the nephridial system in the first ten segments (semi-diagrammatic). *cg*, cerebral ganglia; *f*, pre-septal funnel of the nephridium of the seventh segment; *giz*, gizzard; *is* 1/2, *is* 4/5, *is* 5/6, *is* 6/7, intersegmental septa separating the several numbered segments; the septum 5/6 covering the gizzard is cut to expose a part of the gizzard and the nephridia of the third, fourth, and fifth segments on the right side; *np*³,⁴,⁵, tufted nephridia of the third, fourth, and fifth segments with their respective pre-septal funnels in front, and their vesicular ducts leading to and opening on their respective segments; *np*⁶, tufted nephridium of the sixth segment; *nt*², nephridial tuft of the second segment with its pre-septal funnel between septum 1/2 and the ventral nerve-cord; *oe*, oesophagus; *ph*, pharynx; *vd*², *vd*⁷, vesicular ducts of the nephridial tufts of the second and seventh segments. (× circa 7.)

nephridioblastic rudiments lodged in the septa give rise to a ventral preseptal funnel and a postseptal string of canal cells extending away from the middle line across the segment. Starting from the farther end of the string a succession of loops is developed each of which eventually grows into a separate



TEXT-FIG. 73 B.

Eutyphoeus waltoni, inner view of trunk segments of embryo after removal of gut; showing integumentary meronephridial loops (1-8) on postseptal cord of cells, *nc.* *fr.*, rudiment of funnel of large exonephric ventral meronephridium; *n.*, dorsalmost already separated integumentary meronephridium; *is*, intersegmental septum; *ss*, setal sacs; *vnc*, ventral nerve-cord (Bahl, 1942).

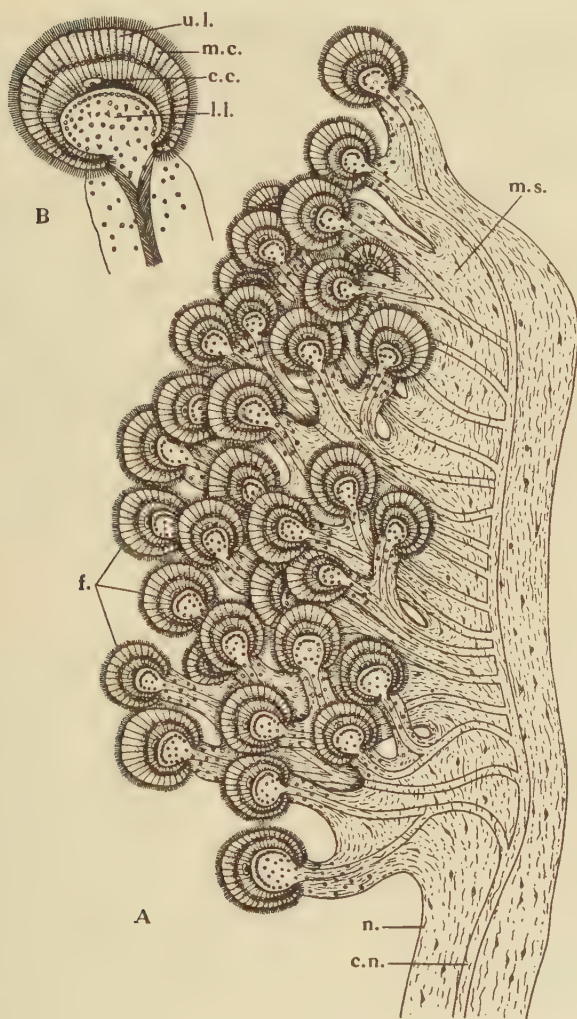
meronephridium without funnel (Text-fig. 73B). The residual portion with the funnel near the middle line belongs to the permanent large open meronephridium (so-called meganephridium) of the adult. These observations also agree with his general account of the development of nephridia in *Pheretima* (see p. 271).

Meronephridia, then, whether integumentary or septal or pharyngeal, are formed by the subdivision of paired holonephridia in the course of development.

The Plectonephric Condition.—It was at one time

believed (p. 244) that in earthworms with many nephridia per segment there existed on the inner side of the body-wall an anastomosing plexus of canals joining them together, and connecting the nephridia not only in each segment but also from segment to segment (Beddard, Spencer, Benham). Further, Beddard (1888) suggested that such a 'diffuse' or 'plectonephric' network, which he described for instance in *Perichaeta* (*Pheretima*) *aspergillum*, was primitive and derived from the branching system of protonephridia found in Platyhelminths. But such a view has now been generally abandoned. Already in 1894 Bourne (p. 257) doubted the existence of such a system of anastomosing canals when he confirmed and extended Vejdovsky's account of the development of multiple nephridia (p. 257). Almost all observers since Bourne deny their presence in or on the body-walls (for the special case of *Libyodrilus* see p. 238). Bahl found no such networks in any of the forms he studied except in so far as the enteronephric septal canals may be joined together from segment to segment by longitudinal collecting canals in the dorsal intestinal wall. The conception of a plectonephric system may be due to the misinterpretation of the persistence of canals joining the meronephridia derived from each other by subdivision. Nevertheless it is difficult to dismiss altogether the very explicit statements made by such experienced observers as Beddard and Spencer (confirmed by Bage, 1910) until the species they studied have been thoroughly reinvestigated. This discussion leads us to another subject dealt with below.

Multiple Funnels.—The presence of several fully formed and functional preseptal nephridiostomes belonging to the paired nephridia in the trunk segments was first discovered by Pickford (1940-1) in the Glossoscolecoid *Thamnodrilus crassus* from Ecuador, and later studied by Bahl (1942, Text-fig. 73 c). The funnels, from thirty to fifty in number, vary somewhat in size, but are all complete and of the ordinary type with central and marginal cells in the upper lip. In each group all their canals join to a single canal which pierces the septum. Bahl has further shown that in *Hoplochaetella*



TEXT-FIG. 73 C.

Thamnodrilus crassus (Bahl, 1942). A, The pre-septal multiple funnels of a nephridium. (\times circa 45.) B, A single funnel much enlarged. (\times circa 94.) *cc*, central cell of the upper lip; *cn*, canal of the neck; *f*, funnels; *ll*, lower lip; *mc*, marginal cells of the upper lip; *ms*, membranous shelf of the funnels; *n*, neck of the funnels; *ul*, upper lip.

bifoveata the large septal nephridia are also provided with multiple funnels, but each group consists of only one large and functional and some eighteen to twenty-four small more vase-shaped and vestigial funnels, since they no longer communicate with the canal. Finally, he finds in species of *Megascolex* (*Lampito*) attached to the active preseptal funnels several masses of embryonic cells interpreted as vestigial funnels in various stages of degeneration.

The exact significance of these discoveries seems doubtful. They may indicate that while usually formation of meronephridia takes place by the growth and subdivision of the postseptal region (see Text-fig. 73 B), in other cases growth and subdivision may first occur in the preseptal region. Thus might arise the multiple-funnelled condition, and degeneration of extra funnels might follow. On the other hand, the completion of the process throughout the postseptal region as well would give rise to a group of open meronephridia such as occurs in *Megascolex dubius* (see footnote, p. 257).

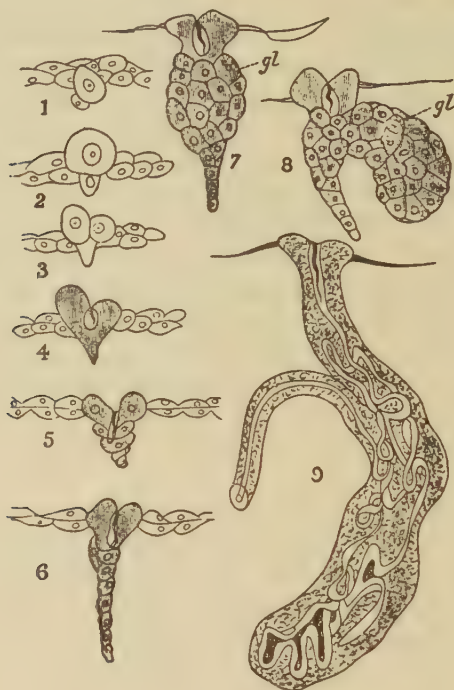
Phylogenetic Origin of Enteronephric Systems.—An interesting problem still remains unsolved. It concerns the phylogenetic origin of enteronephric systems. In the cases of buccal and pharyngeal enteronephridia it has been pointed out that the most anterior exonephridia tend to open more and more inwards, grooves may be formed from the most anterior pores to the mouth, and pores might be, so to speak, drawn inwards by the ingrowing stomodaeum. According to Beddard (1892) in *Octochaetus multiporus* during development the pores of the 'peptonephridia' do pass farther down the stomodaeum. In various *Megascolecidae* there seems to be a transition from a condition where the ducts of the more anterior nephridia reach forward to quite near the mouth, as, for instance, in *Pontoscolex* (Bahl, 1942*a*, Text-fig. 73 A); to a condition like that of *Megascolex cochiniensis*, in which only the foremost nephridia (of segment 5) open into the pharyngeal lumen (Bahl, 1942*a*, Text-fig. 71 B). In *Pheretima*, where three ducts open into the pharynx from segments 4, 5, and 6, the process would have been carried farther (Text-

fig. 70). Plausible as this explanation is, no detailed account has yet been given of how the transference of the pores could take place.

It is more difficult to explain the origin of the intestinal enteronephric system. Undoubtedly the septal nephridia were originally exonephric. The nephridiopores could not be actually transferred to the intestine; but it is possible that there was a transitional stage when by outgrowth from the canal a new connexion was established with the lumen of the enteron, and that the original duct to the exterior was then lost. If Beddard's description of the 'anal nephridia' of *Octochaetus* be correct, they may be taken to represent this stage (see footnote, p. 243). But, at all events, just such a double exit, one through the persisting normal duct and pore and the other through the new longitudinal dorso-lateral collecting duct, has been described by Rosa (1906) in the posterior region of an *Allolobophora antipae* (see p. 239). Only by further research can this problem be solved.

Larval Nephridia.—Provisional larval nephridia have been described by Vejdovsky in various *Oligochaeta*, and by Bergh, in *Criodrilus*. They appear as a pair of simple ciliated canals with intracellular lumen ending blindly internally, and opening by lateral pores on the first segment (or by a median dorsal pore in *Dendrobaena*). More recently in *Rhynchelmis* Iwanoff (1928) has described the larval protonephridium as ending internally in a solenocyte-like cell (but with several cilia), and similar organs in *Tubifex* and *Lumbricids*. Hoffmann (1899), however, maintains that in *Allolobophora putris* (*Dendrobaena*?) the larval nephridium opens into the 'Kopfhöhle' (presumably the coelomic cavity of the first segment). It is possible that this organ is the second of the series, really the metanephridium belonging to septum 1/2. Transitory nephridia have been described by Vejdovsky (1887) in anterior segments of several *Oligochaeta*. In *Rhynchelmis*, he states (1889-92), they pass through a 'pronephridial' stage with the internal end closed by a flame-cell, which later divides and opens to form a nephridiostome (Text-fig. 74).

Such metanephridia, like the anterior protonephridia, disappear and are later replaced functionally by the more posterior definitive metanephridia.



TEXT-FIG. 74.

Rhynchelmis. Development of a metanephridium showing successive stages 1-9 from nephridioblast to complete organ with funnel and postseptal lobe, *gl*, containing glandular canal (Vejdovsky, 1888-92; from Beddard, 1895).

Embryonic. Development of the Nephridia.—By 1895 our knowledge of the development of the nephridia and genital ducts of the Oligochaeta was fairly complete (Bergh, 1888, 1890; Vejdovsky, 1879, 1884, 1887), and was summarized as follows: 'The nephridia of the Oligochaeta are probably of epiblastic origin. They develop from large cells ("funnel-cells"), arranged metamerically outside and between

each pair of somites. They pass through a more or less disguised pronephridial stage (comparable to that permanently retained in flatworms, &c.); in the first segment (most forms), and sometimes in the trunk segments (*Chaetogaster*, and "closed" nephridia of *Megadrili*) they never develop beyond this stage. In the other segments the nephridia grow towards, and open into, the coelom by means of a funnel formed from the original "funnel-cell". (Goodrich, 1895, p. 492.) (Text-fig. 74.)

'The genital ducts, on the other hand, are peritoneal funnels of undoubted mesoblastic origin, which grow outwards from the metameric genital follicles to open to the exterior. They thus have no connexion with the nephridia, and differ from them entirely in their development.' (Goodrich, 1895, p. 492.)

These conclusions were founded mainly on the final opinion of Vejdovsky (1888-92), but there were still many discrepancies between the accounts of the various authors. For instance, Wilson and Vejdovsky derived the nephridia from superficial teloblastic rows of cells considered to be ectodermal. But, while Vejdovsky derived the whole organ, funnel and canal, from the cell-row, Wilson derived the funnel from the coelomic epithelium and the canal from the cell-row. Bergh maintained that the 'funnel-cells' were each derived independently from the coelomic epithelium.

In 1899 Bergh returned to the question in a study on the Lumbriculid *Rhynchelmis*. According to him the large 'Trichterzelle', to which he gave the name *Nephridioblast*, appeared in the coelomic epithelium on the anterior face of a septum, and thus was of coelomesoblastic origin. It gave off a series of cells posteriorly from which developed the canal, and divided to form the four cells of the lower lip of the funnel. The origin of the eight ciliated marginal cells of the upper lip appeared to be doubtful, but Bergh believed them to be derived from the coelomic epithelium. The cavity of the funnel was an extension from the coelom, later prolonged to form the intracellular lumen of the canal. Meanwhile a flagellum working inwards appeared inside the funnel (its attachment was not precisely described). Bergh reiterated his statement, founded

on his earlier work on *Lumbricus* and *Criodrilus*, that the nephridioblasts originated separately (not from superficial teloblastic rows as held by Wilson and Vejdovsky), and gave rise to the whole of the nephridium including funnel and bladder (but probably excluding the upper lip marginal cells).

Staff (1910) in the embryo of *Criodrilus* (closely allied to the Lumbricidae) described four teloblastic rows which come to lie on the inner surface of the covering epidermis. The first, most median and ventral, is the neural row; the second is the nephric row; the third and fourth give rise to the circular muscles. The nephric row is said to become broken up progressively from before backwards into separate segmental groups of cells, the rudiments of the nephridia. The large anterior cell of each group ('Trichterzelle' or nephridioblast) comes to project on the anterior face of a septum, and gives rise to the upper lip of the funnel, the lower lip being formed from more posterior cells of the rudiment. Briefly, Staff derives the whole nephridium from originally retroperitoneal rudiments developed from an ectodermal nephric row produced by a posterior teloblast. He thus confirms Vejdovsky's conclusion.

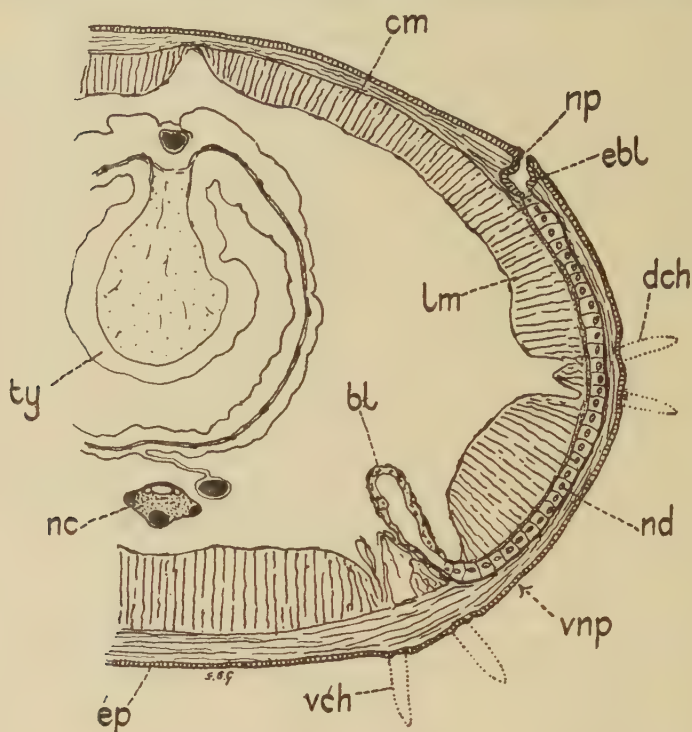
Later authors have, however, not supported this view. The most detailed description of the development of the metanephridium of a Lumbricid is that given by Vanderbroek (1934) in *Eisenia foetida*. He traces the whole organ, from funnel to pore, from a single nephridioblast found on the anterior face of the septum on each side in each segment. This large cell by repeated division buds off a string of cells posteriorly, the rudiment of the canal, which grows back between ectoderm and coelomic wall. Later this post-septal region bulges into the coelom carrying a covering of coelomic epithelium with it. The hinder end of the string extends between the developing longitudinal muscles within and the developing circular muscles without, then reaches the surface piercing the epidermis to open by a pore. This nephridiopore may be either ventro-lateral, lateral, or dorso-lateral, and the embedded duct leading to it is correspondingly lengthened, the attachment of the nephridium to the inner face of the body-wall being always ventro-lateral.

Vanderbroek shows clearly that the bladder (vesicle) is derived from the originally continuous string of cells, and not from a late invagination of ectoderm. I am able fully to confirm this conclusion from my own observations on *Lumbricus*, and there can be no doubt that Bergh (1899) was right in maintaining, as against Vejdovsky (1900) (who believed the vesicle to be an epidermal invagination), that the whole nephridial canal is derived from the nephridioblast (Text-fig. 75). But Vanderbroek goes farther, and, if I understand him rightly, holds that there is scarcely any invagination at all at the pore. My own observations on *Lumbricus* seem to show that, while the inner wall of the small 'ampulla' situated in the adult in the circular muscle layer, is derived from the canal itself, the outermost part of this wall and the short wide duct leading to the surface is lined by cuticle and due to an ingrowth of epidermis. Another small point concerns the structure of the embedded duct leading from vesicle to ampulla. My sections show that it is not, as Vanderbroek says, 'tapissé par un épithélium pavimenteux'; but contains an intracellular lumen piercing a regular series of drain-pipe cells until it reaches close to the ampulla (Text-fig. 75).

More important is the fact that in his well-illustrated account Vanderbroek traces the origin of the whole nephridiostome of *Eisenia*, including both upper and lower lip, from the products of the nephridioblast. The central and marginal cells of the upper lip are, according to him, derived from the most anterior or last-formed cell of the posterior cell row, while the lower lip is formed by the final divisions of the residual nephridioblast itself. Thus, he fully confirms my own account of the development of the whole nephridiostome of *Lumbricus* (except, of course, the outer covering of coelomic epithelium and the thin intermediate layer of connective tissue) from cells of nephridioblastic origin (Goodrich, 1932). In my detailed account of the nephridiostome it is shown that evidence of this origin is not only to be found in development, but also in the histological structure of the funnel cells in the adult (Text-fig. 65).

When we come to Vanderbroek's account of the ultimate

origin of the nephridioblast itself his evidence is less conclusive. He maintains that this large cell appears in the postero-ventral



TEXT-FIG. 75.

Lumbricus sp. Transverse section (reconstructed from three consecutive sections) showing nephridial duct, *nd*, from *bl*, bladder, to epidermal ingrowth, *ebl*. The duct is formed of a series of drain-pipe cells with intracellular lumen. *cm*, circular muscles; *dch*, dorsal chaetae; *ep*, epidermis; *lm*, longitudinal muscles; *nc*, nerve-cord; *np*, nephridiopore; *ty*, typhlosole in intestine; *vch*, ventral chaetae; *vnp*, position of ventral nephridiopore on another segment. Enlarged.

angle of the coelomesoblastic somite, that it may be distinguished before the coelomic cavity is formed and even before the coelomesoblastic band becomes divided into segmental blocks (this I can confirm), as a pronephridioblast capable of giving off by

division a few cells destined to form coelomic epithelium. He considers, like Bergh before him, the nephridioblast to be a coelomic epithelium cell specialized to give rise to the whole nephridium.

But, although it is no doubt true that the nephridioblast may be recognized embedded in the coelomesoblast at a very early stage, it does not necessarily follow that it really belongs to this layer. Vanderbroek does not seem to me to have settled this difficult but most important point. Vejdovsky (1892), after many years' study, concluded that the nephridioblasts in Lumbricids are derived from a nephric row of cells produced by a nephro-teloblast. Later Staff (1910) came to the same conclusion, as mentioned above, also Bahl more recently (1922) in the case of *Pheretima* (see p. 273).¹

Another important contribution is that of A. Meyer on the development of the nephridia in *Tubifex rivulorum* (1929*a*). Having severely criticized the work of Penners, who derived the nephridia from the coelomesoblast (1924), and corrected some of his errors, Meyer gives a clear and well-illustrated account of the development of the nephridia from the time when the nephridioblast can be seen as a large cell on the anterior face of the septum in the segments behind the genital region (Text-fig. 76). He describes the production from it of the post-septal string of cells, the growth of its posterior end into the epidermis to open to the exterior, the appearance of the intracellular lumen, and the formation of the nephridiostome with its four nuclei by the division of the residual nephridioblast or funnel cell. From my own observations I can fully confirm these observations.

But it is when Meyer claims that the nephridioblast is a cell of the coelomic epithelium that his evidence is insufficient (as

¹ It would appear from these authors' works, and also from my own experience, that only quite early embryonic stages are suitable for the study of the nephric rows and the origin of the nephridioblasts. In later stages the cells become too numerous and too closely packed. Vanderbroek seems to have studied chiefly stages far too advanced—in the one he figures some eighty segments are already laid down, and the coelom has begun to appear in the forty-fourth segment. Moreover, he gives no detailed account of the fate of the lateral teloblastic rows.



TEXT-FIG. 76.

Stages in development of nephridium of *Tubifex rivulorum*, *a-g*. Septa 13/14, 14/15, 15/16, 16/17. Fig. *h*, young nephridio-stome with two nuclei. Fig. *i*, later stage with four nuclei. *D*, septum; *m*, nuclei of septal muscle cells; *p*, coelomic epithelium (A. Meyer, 1929).

already pointed out in a footnote, p. 176, in my paper on the nephridiostome of *Lumbricus*, 1932). In the stages figured the structures concerned are already far advanced, the coelom is extensive, the septa are thin, and the large single nephridioblast on each side necessarily projects on the anterior surface of the septum; but this in no way decides whence it has been derived.

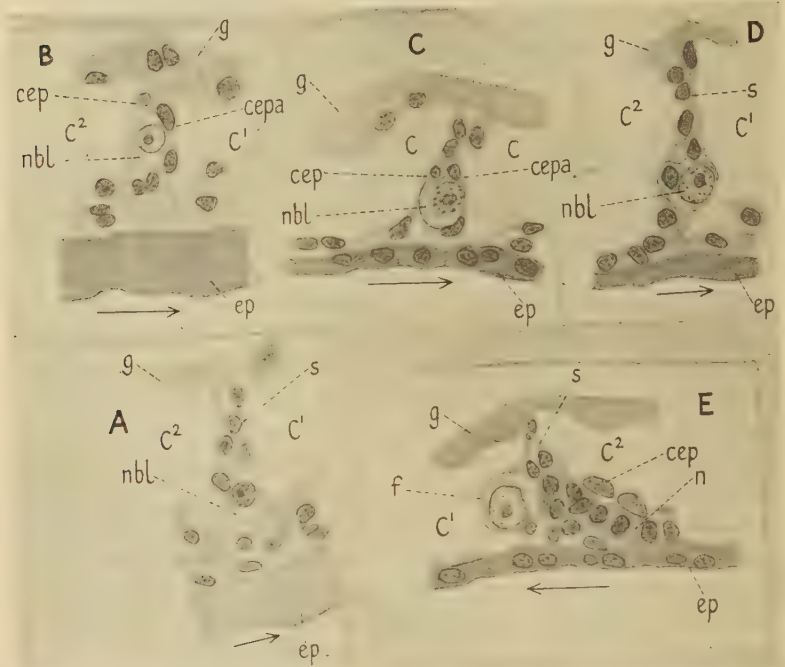
In the attempt to solve this difficult problem I have carefully studied earlier stages in *Tubifex*, and find that, in segments farther back and therefore less advanced than those in which the nephridioblast occupies a position in the preseptal coelomic epithelium and is exposed to the coelomic fluid (as in Meyer's figures 18, 19, and 20a here reproduced as Text-fig. 76), the nephridioblast can still be identified both in whole preparations and in sections. In such earlier stages the nephridioblast, as shown in Text-fig. 77, is embedded in the thickness of the septum and is covered both anteriorly and posteriorly by coelomic epithelium cells.¹ It is in fact retroperitoneal and inter-segmental in position. Although able to follow the nephridioblasts for many segments farther back towards the growing posterior end of the embryo, I have unfortunately not as yet succeeded in tracing their first origin. But that they are not merely converted cells of the coelomic epithelium there can be no doubt.

Tannreuther's account of the origin of the nephridia in *Bdellodrilus* from superficial nephric rows (1915) is too incomplete to be conclusive; but Bahl (1922) has made an important contribution to the evidence brought forward by the supporters of our interpretation in his work on the development of the complex nephridial system in *Pheretima* already dealt with above (Text-fig. 78).

Bahl has shown that at a stage with about fifty segments the first nephridia to develop are a pair of primary integumentary nephridia in every segment from the seventh backwards (Text-

¹ This confirms the observations of Vejdovsky (1884) who described and figured the nephridioblast at this stage as being more on the posterior than on the anterior side of the septum which is covered by ordinary flattened coelomic epithelium (Text-fig. 74).

fig. 78). In the quite early embryo, when the deep-lying coelomesoblast band is beginning to segment and its anterior somites

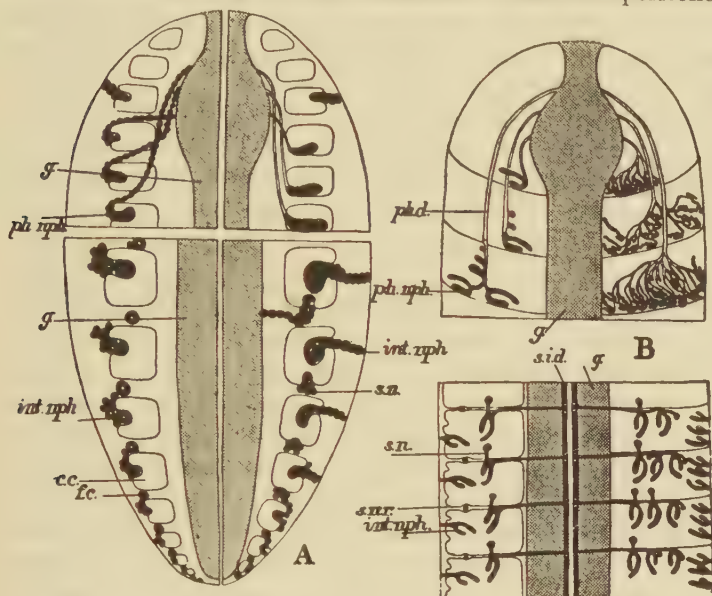


TEXT-FIG. 77.

Tubifex rivulorum. Longitudinal sagittal sections showing relation of nephridioblast to intersegmental septum, *s*, in successive stages from A, *s* 20/19; B, *s* 19/18; C, *s* 14/13; to D, *s* 13/12. In A and B nephridioblast, *nbl*, in middle of septum; in C it is bulging forwards, and in D is breaking through coelomic epithelium; E, similar section of older stage. *c*^{1,2}, consecutive coelomic cavities; *cep*, coelomic epithelium of posterior face, and *cepa*, of anterior face of septum; *ep*, epidermis; *f*, funnel cell (residual nephridioblast); *g*, wall of gut; *n*, row of nephridial cells.

already show small coelomic cavities, the more superficial teloblastic rows are clearly visible with their four large teloblasts situated at the surface. The rows in front of them gradually sink below the epidermis. The products of teloblasts two and three combine to form a nephric band extending between

epidermis and coelomesoblast. Some cells from this band then push their way into the septa passing between the opposing walls of two adjoining coelomic chambers. These retroperitoneal



TEXT-FIG. 78.

Pheretima. Diagram showing common origin from posterior nephridial teloblasts of three kinds of nephridia in embryo. A, younger and B, later stage. cc, coelomic cavity; fc, funnel cell; g, gut; *int.nph*, integumentary nephridium; *ph.d*, duct of pharyngeal nephridium, *ph.nph*; *s.i.d.*, supra-intestinal excretory duct; *sn*, septal nephridium; *snr*, rudiment of *sn* (Bahl, 1922).

intersegmental groups of cells, situated where the septa join the body-wall, are the rudiments from which develop the nephridia. To form the primary integumentary nephridia the rudiment grows posteriorly to the septum, and bulges from the body-wall into the coelom. A twisted and looped string of nephridial cells is formed which acquires an intracellular ciliated lumen. The rudiment shows no persisting anterior large 'funnel-cell', since no funnel is formed and the nephridium remains blind in the adult. The other end grows through the body-wall to open to the exterior. In those segments (from

septum 15/16 backwards) where septal nephridia occur, the original rudiment divides into two groups of cells. The more posterior develops into primary integumentary nephridia, as just described; while from the more anterior retroperitoneal cell group one cell passes dorsally into the septum, and forms the rudiment of the primary septal nephridium.

In such a rudiment develops a coiled string of cells having at one end the residual nephridioblast, or large funnel cell destined to form the nephridiostome including both upper and lower lip. The other end grows inwards in the septum and parallel to the commissural blood-vessel to reach the intestine below the median dorsal vessel, and finally to open into the intestinal cavity at the side of the typhlosole. The funnel end and the nephridial canal come to project on the anterior face of the septum, attached to it by a septal canal.

The origin of the numerous 'secondary' integumentary nephridia which appear scattered over the body-wall is not so clearly determined. They arise as retroperitoneal cells derived from the primary groups, or possibly from cells which have independently migrated from the nephric bands. The 'secondary' septal nephridia develop from nephridioblasts migrating successively into the septum from the original intersegmental group which gave rise to the primary septal nephridium. Each nephridioblast forms a rudiment with a funnel cell and a string of canal cells. The funnel cell comes to project either on the anterior or the posterior face of the septum, and eventually breaks through the coelomic epithelium and forms an open nephridiostome. At the opposite end of the string the canal cells of each newly formed rudiment grow out as a duct which joins those of the preceding septal nephridia, thus combining to form the definitive septal excretory canal emptying into the intestine. By the backward growth and junction of these canals along the roof of the intestine are formed the continuous paired longitudinal ducts which open intersegmentally into the gut.

The pharyngeal nephridia develop also from cells derived from the nephric rows. Each rudiment so formed in segments 4, 5, and 6, gives rise to a string of cells passing forwards to the pharynx. These ducts soon acquire an intracellular lumen and

open into the pharynx. Meanwhile the groups of cells forming the bodies of the nephridia become related to the septa behind them. Buds growing out of these rudiments give rise to the 'secondary' pharyngeal nephridia whose ducts open into the primary ducts. So are developed the tufts of pharyngeal nephridia without funnels in segments 4, 5, and 6.

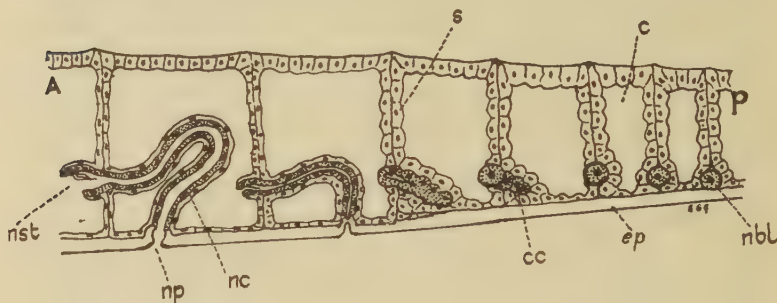
Thus all the various nephridia have a common origin. Primary nephridioblastic teloblasts give rise to nephric bands, and these give rise to secondary nephridioblasts which are distributed to the successive segments where they take up a retroperitoneal intersegmental position in the septa (Text-fig. 78).

Summary.—From the analysis given above of recent work on the development of the nephridia in the Oligochaeta, it may safely be concluded: that it is now definitely established that the whole nephridium from funnel to pore (including the whole nephridiostome, the excretory canal, the bladder and duct to the exterior, but excepting an insignificant ingrowth of epidermis at the pore in higher forms), arises from a special cell, the nephridioblast; that the nephridioblast does not belong to the coelomic epithelium, is not derived from the coelomesoblastic band, but is of retroperitoneal origin, primitively occupies an intersegmental position, and only breaks through the coelomic epithelium at the point where the nephridiostome comes to open (Text-fig. 79).

Further, it is exceedingly probable, though not so definitely proved, that such nephridioblasts are derived in the higher Oligochaeta (Megadrili) from nephric bands or rows of cells formed by the repeated forward division of posterior nephric teloblasts situated at first in the surface layer of ectoblast; or, if not from regular bands, at all events from originally superficial cells of ectodermal or ectomesodermal nature.

Usually, and possibly always, the nephridial canal develops as a string of cells, produced by the repeated backward division of the nephridioblast, which string becomes hollowed out by an intracellular lumen. The nephridiostome is formed by the division of the residual nephridioblast itself, though some of the most anterior cells of the string may contribute to it.

In this connexion it must be remembered that, like the larval protonephridia of the Polychaeta, the larval nephridia of the first segment in Oligochaeta appear certainly not to be developed from the coelomesoblast, but from ectoblastic or ectomesoblastic cells (cells 2*c* in *Bimastus*, according to Svetlov (1928)). They appear very early and in *Tubifex* even before the



TEXT-FIG. 79.

Diagram of development of metanephridium in Oligochaeta. A, Anterior. P, Posterior. c, coelom; cc, canal cells; nbl, nephridioblast; at, first intersegmental later bulges into segment in front; nc, nephridial canal covered with coelomic epithelium; np, nephridiopore; nst, nephridiostome; s, septum.

coelomesodermal teloblast has begun to divide (Ivanow, 1928). It may be concluded that, as long ago maintained by Vejdovsky, neither the embryonic nor the later nephridia are derived from the coelomesoblast.

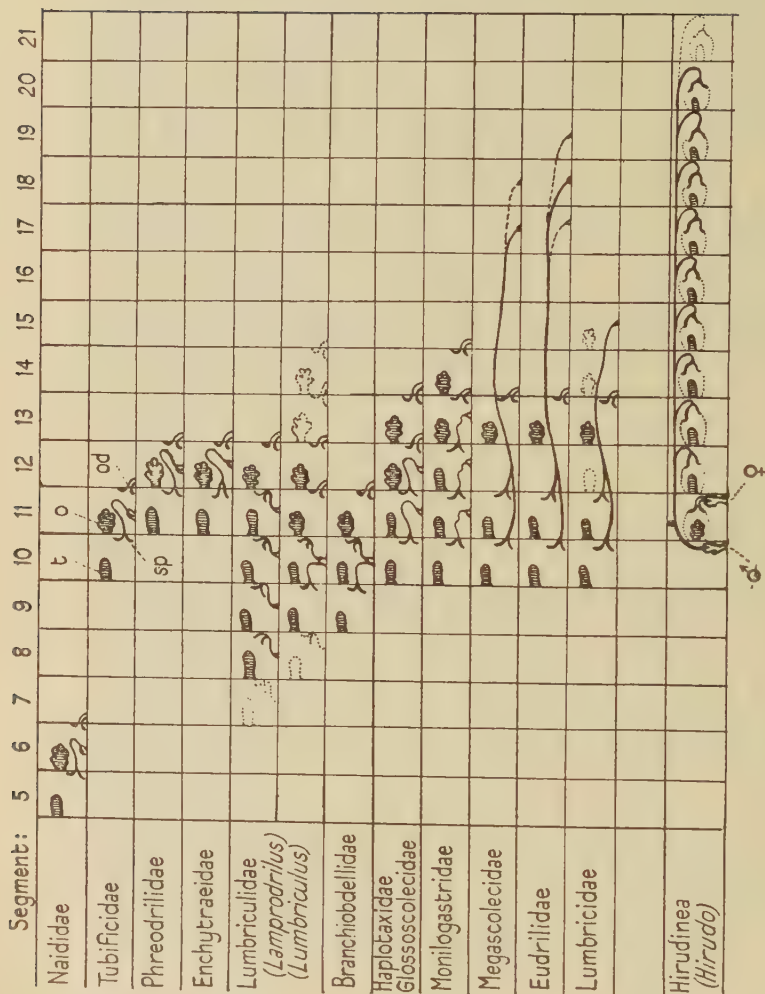
The Genital Ducts.—There remains the question of the homology of the genital ducts in Oligochaeta, and their possible relation to the nephridia. Since 1895 more evidence has been brought forward for the view (Goodrich, 1895) that these ducts are quite different from the nephridia in phylogenetic origin and in development, being typical coelomoducts formed as outgrowths from the coelomesoblastic wall of those segments in which gonads are present.

An excellent account of the genital organs of these hermaphrodite annelids will be found in Stephenson's Monograph

(1930). Although differing much in detail in the various families, they conform to a general plan uniform throughout the Class.

The tendency seen in other Annelida for the gonads to become restricted to the segments of the middle region of the body, while the other segments remain sterile at either end, is carried to an extreme in Oligochaeta where (except in abnormal individuals) never more than four pairs of testes and never more than three pairs of ovaries normally occur. The ovaries always follow close behind the testes: usually one pair of the former, and one or two of the latter. The coelomoducts likewise are reduced to correspond exactly in number and position to the gonads (Text-fig. 80).¹ The latter project into the coelom from the posterior face of the anterior septum of the fertile segments, and the ciliated coelomostomes open opposite on the anterior face of the next septum behind. The duct pierces this septum to reach the gonopore. The oviducts remain simple, and open on the next segment; they may be reduced to little more than pores in some 'Microdrili'. The sperm-ducts are relatively large and more differentiated, and often provided with special glands and copulatory apparatus. Their coelomostomes, relatively large and well-developed 'sperm-funnels', are followed by a slender post-septal duct. In 'Microdrili' this duct may be much lengthened, and project into the coelom; but, it still opens on the next segment. In 'Megadrili' the sperm-duct usually runs backwards along the body-wall retroperitoneally to open, in the Lumbricid for instance, on the fifteenth, and in the Megascolecid and Eudrilid on the eighteenth segment. Moreover, in these families the two ducts on each side tend to join to a common pore behind. Occasionally the right and left sperm-ducts join to open by a median ventral pore (Tubificids, *Rhizodrilus* (Goodrich, 1895), *Bothrioneuron*; many Eudrilids; the Lumbriculid, *Mesoporo-drilus*; the Megascolecid, *Plutellus*).

¹ The genital ducts may be considered as survivals in certain segments of the continuous ancestral series of coelomoducts, and vary much in position in different Families and even in species and individuals (Text-fig. 80). This variation is great in Lumbriculidae, where it has been studied in detail by Mrazék (1906) and Yamaguchi (1936-7).



TEXT-FIG. 80.

Diagram showing position of gonads and coelomoducts in Oligochaeta and Hirudinea. 5-21 segments; o, ovary; t, testis; sp, sperm-duct. Supplementary organs in dotted lines. Range of sperm-duct in Megascolecidae and Lumbricidae in broken lines.

Some epidermal invagination seems always to occur at the male pore. Usually it is considerable, giving rise to glands, atrium, and copulatory organs.

The early view that the genital ducts are modified nephridia may be traced back to Williams, 1858, but more especially to Claparède who observed that the nephridia are absent from the genital segments of 'Microdrili'. Such a theory could only have been put forward at a time when the development of nephridia was not understood and that of the genital ducts was still unknown.

The disappearance of the nephridia in the genital region of the 'Microdrili' is probably due to the relatively large size of the genital organs in these small worms, and according to Vejdovsky (1884) at least transient rudiments of nephridia may be seen in the genital segments of young stages. They disappear later in the genital, and certain other anterior segments. The regular series of nephridia is uninterrupted throughout the genital region of the larger Oligochaeta, and they remain unaltered in structure.

All the evidence recently derived from the study of the development of the genital ducts confirms the view that they arise from the coelomic epithelium as stated by Vejdovsky (1884), Bergh (1886), Lehmann (1887), and later writers.

Gatenby has given a detailed well-illustrated account of the development of the ducts in *Tubifex*. 'The first sign is found in the multiplication of the coelomic cells on the front of septum 10/11' (Gatenby, 1916, p. 320). This gives rise to a thickening which grows backwards through the septum into segment 11, carrying the epithelium of the posterior face with it. The point of this rudiment of the duct grows along the body-wall to above the ventral bundle of chaetae where it pierces the muscular layers to reach and fuse with the epidermis. The rudiment of the funnel, at first a circular flattened plate, becomes thicker, its cells elongate and acquire cilia, and its edge grows and projects forward more and more to form the lip of the sperm-funnel. At the growing rim the ciliated inner epithelium remains continuous with the flattened coelomic epithelium covering the funnel, and some connective tissue

passes in between the two layers. The solid outgrowing duct having fused with the epidermis acquires an intercellular lumen opening at the pore. The atrium is derived from an ectodermal ingrowth.

The oviduct in *Tubifex* is much reduced, but develops from the coelomic epithelium in essentially the same way. The lumen of the oviduct, however, apparently is only pierced to the outside just before the eggs are laid.

According to Mehra's account (1924) of the development of the sperm-duct in the Naid *Stylaria* it arises from a plate of thickened coelomic epithelium (on the anterior face of septum 5/6) just as in *Tubifex*. From this plate grows backwards through the septum the rudiment of the duct, which eventually meets, in segment 6, an ingrowth of the epidermis giving rise to the atrium.¹

It may be considered as clearly established that the genital ducts in *Oligochaeta* originate from the coelomic epithelium as typical coelomoducts, and that they differ radically from the metanephridia in development (Text-fig. 80). They retain their original function, the metanephridia being excretory and the coelomoducts purely genital, and they never combine to form nephromixia.²

¹ It is strange what careless and misleading statements have been made on this subject. For instance, Michaelsen ('Handb. d. Zool.', Bd. II, H. 2, p. 64, 1932) says that 'Die Ausführorgane entstehen auf ganz ähnliche Weise wie die Nephridien selbst' (!). While Vanderbroek (1934, p. 67) commenting on the difference between nephridia and coelomoducts, states that 'En démontrant l'origine mésodermique des néphridies, nous avons prouvé que, chez les Oligochètes, cette distinction n'est pas fondée et ne correspond à rien de réel. Le néphridioblaste est donc lui aussi un coelomoducte, l'entonnoir vibratile un coelomostome.' Ignoring the older writers and Gatenby's recent paper, he cites only Mehra on organogeny, and states that 'les conduits génitaux se forment aux dépens du péritoine, suivant un processus identique à celui qui préside à la formation d'un néphridioblaste. Ces organes sont homologues.' Mehra himself (1924, p. 165) says 'Now it is clear beyond doubt . . . that the genital ducts are quite different in origin from the nephridia'.

² It must, however, be mentioned that Beddard (1892) believed that the genital ducts were derived from nephridia, and that Benham (1904) suggested that *Haplotaxis heterogyne* is remarkable among *Oligochaeta* in that its sperm-duct is a nephromixium composed of a coelo-

Class Hirudinea.

It is now realized that the Class Oligochaeta and the Class Hirudinea are very closely allied. Indeed, Michaelsen unites them in the one group Clitellata.

Our knowledge of the minute structure of the nephridium (a metanephridium) of the Hirudinea is mostly founded on the early work of A. G. Bourne published in this Journal from 1880 to 1894 (vols. 20, 22, 24, 34). Since then it has been extended, and in some respects corrected, by various authors, more especially by Oka (1894), Bolsius (1889-1900), McKim (1895), Graf (1893, 1894, 1899), Loeser (1909), Bhatia (1938).

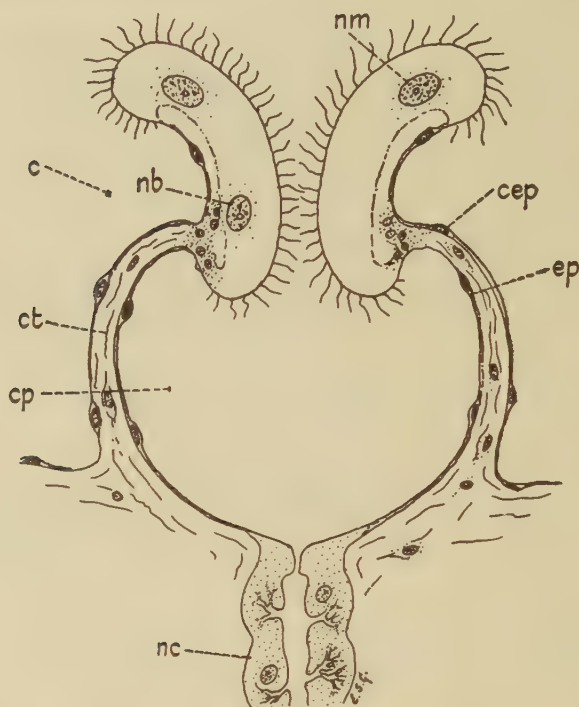
The nephridium is built on the same general plan as the metanephridium of the Oligochaeta; but it is much specialized, partly owing to the great reduction of the coelom which in most Hirudinea is represented by a system of communicating narrow channels and some larger spaces, the so-called lacunae or sinuses.¹

The nephridiostome projects freely into a ventral 'perinephrostomial sinus' or coelomic chamber (ampulla), the remainder of the nephridium being embedded in the connective tissue parenchyma which has to such a great extent invaded the coelomic cavity. The nephridium is characteristically

mic funnel fixed on to a nephridial duct. For this interpretation he relied on the fact that the duct springs from the ventral margin of the genital funnel instead of the more central region, and that the sperm-duct itself resembles in structure the canal of the nephridium. But it must be remembered that both coelomoducts and metanephridia are essentially tubes leading from coelom to exterior, and must perforce be somewhat alike. Moreover, Forbes found separate vestigial nephridia in the genital segments of an immature *Haplotaxis*. The case is far from convincing, and could only be accepted on strong embryological evidence. As it is Benham's evidence is quite inadequate, and will not bear the weight imposed on it. I have to thank him for sending me his sections for inspection.

¹ There can be little doubt that the metanephridium is originally intersegmental in position as in other Annelida, but this is often difficult to make out in the adult Hirudinea, where secondary annulation replaces primitive external segmentation, and coelomic chambers and septa are obscured. In such forms as *Protoclepsia*, however, the opening of the funnel in one segment and the pore on the next segment behind can be made out (Hotz, 1938).

specialized: in the adult the nephridiostome no longer opens into the lumen of the canal but into a 'capsule' (see below); the lumen of the much coiled tube or canal is throughout intra-



TEXT-FIG. 81.

Diagram of nephridiostome and capsule of a Glossiphoniid projecting through wall of ampulla (partly from Hotz, 1938). *c*, coelomic cavity of ampulla; *cep*, coelomic epithelium; *cp*, cavity of capsule; *ep*, lining nephridial epithelium of wall of capsule; *nb*, nucleus of basal cell; *nc*, nephridial canal cell; *nm*, nucleus of marginal cell.

cellular and never ciliated; the only parts bearing cilia are the cells of the funnel itself in all Hirudinea, and the cells of the epithelium lining the terminal bladder opening to the exterior in the Hirudinidae and Herpobdellidae. In these families the bladder is large and provided with sphincter muscles near the opening.

The canal consists throughout of a string of cells (the inter-cellular wall separating them being more or less obliterated) and it is characteristic that, along a considerable length of the first region following the nephridiostome, the main central lumen gives off in each cell side branches ramifying towards its periphery and ending in very fine collecting canaliculi or ductules. The main lumen may also sometimes be subdivided to join again. A similar branching or subdivision of the lumen is known in certain Oligochaeta (*Enchytraeus*, Goodrich, &c., Text-fig. 66, 1896), and side branches ramifying in each successive cell, very like what occurs in the leeches, have been described for instance in *Moniligaster* by A. G. Bourne (1894).

But the most distinctive specialization is in the region of the funnel. The nephridiostome in the Glossiphoniidae, which appear to be the most primitive in this respect, is composed of a ring of a few large ciliated cells leading by a narrow central opening into a wide sac (funnel-sac or capsule) against which abuts the extremity of the nephridial canal. In *Glossiphonia* (Clepsine) one pierced cell forms the duct, and two expanded cells the diverging lips of the funnel (Text-fig. 81). The sac becomes filled with phagocyte leucocytes drawn in from the coelom by the ciliary current.¹

An interesting specialization occurs in the Ichthyobdellidae where an apparently true 'plectonephric' condition becomes established, as long ago described by Bourne (1884) in *Pontobdella* and other genera. Possibly it arose from the intracellular branching of the lumen found in leeches generally. According to Johannsson (1898) while large paired unbranched nephridia are still found in *Cystobranchus*, each pair is joined across by fine branches in *Piscicola*. In *Abranchus* are added longitudinal connexions, and finally in *Pontobdella* the ten pairs of nephridia (situated in segments 9 to 18), still indicated by ten pairs of funnels and nephridiopores, are all connected together by a close network on the inner side of the muscular body-wall. The funnels and funnel sacs resemble those of Glossiphoniidae.

¹ A similar sac or capsule is found in the Oligochaete *Pontoscolex* (Bahl, 1942*a*; see Text-fig. 73).

In *Herpobdella* (*Nephelis*) the large ciliated nephridiostomal cells form a ring or crown round the opening leading into the capsule filled as usual with phagocytes (Loeser, 1909). Both funnel and capsule lie freely in a well-defined coelomic chamber or ampulla attached to its wall only by a few supporting strands. The coelomic epithelium is reflected over the outer surface of both strands and capsule.

The funnel of the Hirudinidae resembles that of the *Herpobdellidae* in essentials, but has become greatly complicated owing to the multiplication of the nephridiostomal cells which come to form numerous isolated secondary funnels opening separately into the much enlarged capsule or 'reservoir' (Text-fig. 82). This capsule becomes elongated and branched, and there is a corresponding enlargement and partial subdivision of the surrounding ampulla (Bhatia, 1938). It is to be noted that in *Herpobdella* each nephridium, except the first, is provided with two ampullae and funnels, presumably owing to the complete subdivision of the original one.

Although the funnel in Hirudinea becomes almost unrecognizably modified there can be no doubt that it is a true nephridiostome (see development, p. 290 and footnote 1). With the formation at its base of the capsule there is developed in leeches a 'cilio-phagocytal organ' remarkably similar to that formed in connexion with the modified coelomostome ('ciliated organ')¹ in certain Polychaeta (p. 200) and fulfilling much the same function. In both cases there is usually no direct communication between the cavity of the phagocytal sac (capsule) and the lumen of the nephridial canal, and the excretory products gathered by the phagocytes appear to reach the canal only in solution by osmosis.²

¹ Though often called the 'ciliated organ', the nephridiostome of Hirudinea should not be confused with the specialized coelomostome to which I applied the name 'ciliated organ' in Polychaeta. There can be no homology between the two organs.

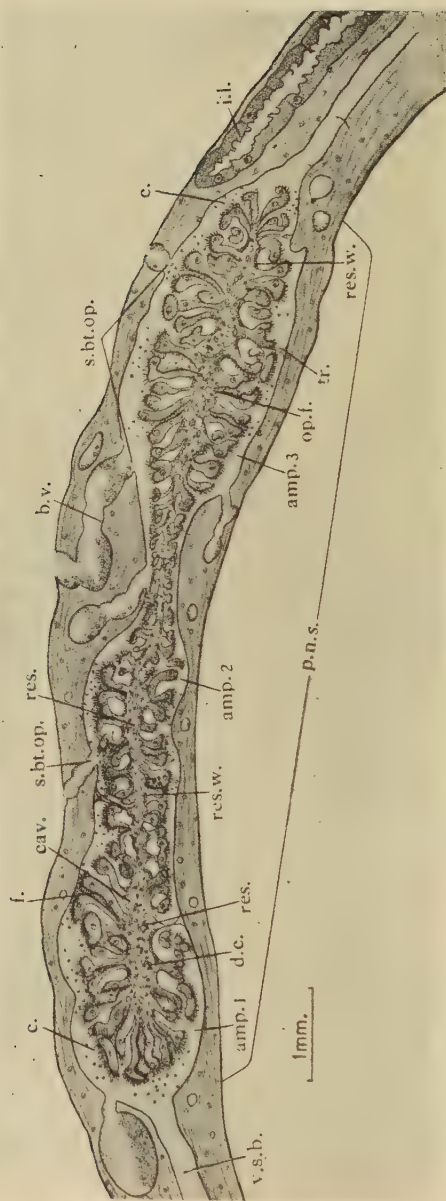
² In connexion with this it may here be mentioned that there has been much controversy as to whether or not the lumen at the extremity of the nephridial canal opens into the capsule in adult Hirudinea. Leuckart (1891-4, 1900), Oka (1894), and McKim (1895) believe that it does; but Bolsius (1894), Graf (1899), Willem and Minne (1900), and Loeser (1909)

The question arises as to the origin of the capsule in leeches. Is it due to the expansion of the extremity of the nephridial canal immediately following the funnel, or is the canal here interrupted and the capsule formed from the coelomic epithelium originally covering the outer surface of the funnel and initial cell of the canal? This point requires further study¹; but the former seems to be the correct view.

There has also been difference of opinion about the function of the capsule. Some observers consider that it contains merely phagocytes loaded with waste products, others that it is a seat for the origin of new corpuscles, or that both functions may coexist. That excretory products are gathered into the capsule there can be no doubt (see, for instance, Kowalevsky, 1897, 1900); but it also appears well established that leucocytes multiply in it by mitotic division. That new leucocytes arise

maintain that it does not in Glossiphoniidae. A communication is also denied in Herpobdellidae, where indeed the canal does not reach the capsule, by Bolsius, Willem and Minne, and Loeser. These authors and Bhatia (1938) likewise deny it in Hirudinidae. From my own observations I am inclined to believe that Bourne was right in saying that the lumen opens into the capsule in Pontobdella. Recently Hotz (1938) has studied the question in detail in *Protocleipsis*. He describes and figures the communication of the lumen of the canal with the cavity of the capsule by several small openings. This result has been incorporated in the diagram here given of the whole apparatus in Text-fig. 81.

¹ If I understand him rightly, the latter is the view held by Graf, who figures the inner lining of the capsule ('receptaculum') in *Glossiphonia* as continuous with the coelomic epithelium covering the outer surface of the funnel cells (his figs. 16 and 17, Pl. III, 1899). There seems to be some misconception here as he labels this flat epithelium 'bd, Bindegewebe Hülle'. According to Graf the initial cell of the canal becomes filled with excretory products, expands, and finally breaks down leaving its covering to form the adult capsule. This view is not consistent with the careful description of Loeser (1909), who figures the wall of the capsule as lined with an inner epithelium continuous not with the covering coelomic epithelium but with the funnel cells. The interpretation of Loeser agrees with my own observations, and with those of Hotz (1938) on *Protocleipsis* where the wall of the capsules consists of three layers: outer coelomic epithelium, middle connective tissue, and inner epithelium of presumably flattened nephridial cells, Text-fig. 81. The capsule, then, is due to the expansion of the anterior end of the nephridial canal immediately following the nephridiostome.



TEXT-FIG. 82.

Hirudinaria granulosa. Longitudinal section of coelomic ampullae, *amp.*^{1,2,3}, enclosing extended capsule, *res.*, and secondarily multiplied funnels, *f* (subdivided nephridiostome). *bv*, botryoidal vessel; *c*, corpuscles; *cav*, cavity of capsule (reservoir); *i.l*, initial lobe (blind end of nephridial canal). The whole perinephrostomial sinus, *pns*, overlies testis sac (Bhatia, 1938).



TEXT-FIG. 82 A.

Hirudinaria granulosa. Ciliated funnels, representing subdivided nephridiostome, removed from perinephrostomial coelomic sinus, cp. previous figures (Bhatia, 1938). *c.a.* cilia; *f.* funnel; *n.* nucleus.

from its wall seems not yet to have been proved. In Hirudinidae (Loeser, Bhatia), at all events, the capsule contains many dividing and healthy corpuscles, a kind of connective tissue, and fine radiating fibres of doubtful meaning (also abundant in *Pontobdella* (Bourne)). Recently Bhatia (1938) has maintained that in Hirudinaria the action of the cilia of the funnels is outwards, the current carrying corpuscles from the capsule into the surrounding coelomic ampulla.

The number of nephridia varies in different species. Usually in the adult they are absent in several anterior and posterior segments, and often also in some clitellar segments.¹ Bergh (1885) has described the development of transitory nephridia in the anterior segments of the embryo of *Aulostoma* (*Haemopsis*). These provisional organs have no funnels or capsules. Funnels and capsules appear to be altogether absent in *Acanthobdella* (Kowalevsky, 1896; Livanow, 1906), and are also usually absent in some of the anterior nephridia of most adult leeches. Such a defect in the adult would seem to indicate rather degeneration than the retention of a primitive protonephridial condition. Sukatschoff (1900), however, describes the end-cell of the provisional 'Urnieren' of *Herpobdella* as very like a flame-cell but without cilia.

The genital organs are remarkably uniform throughout the Class. All leeches are hermaphrodite, provided with one pair of ovaries, in the third clitellar segment generally counted as the eleventh or twelfth segment, and several pairs of testes segmentally distributed in a varying number of segments following behind that bearing the ovaries (from four to eighteen pairs of testes, but usually about twelve). The genital pores are typically median and ventral; the female pore on the segment enclosing the ovaries, the male pore on the segment in front of it.

¹ In the adult *Glossiphonia complanata* (Brumpt, 1900) there are fourteen pairs opening on the first ring of segments 8, 9, 10, and 14 to 25. The first pair is vestigial, and also those in segments 11 and 12 which contain the genital pores.

According to Leuckart (1901), of the twenty-four pairs which appear in the young *Hirudo* three posterior and four anterior pairs are lost, leaving in the adult seventeen pairs in segments 6 to 22.

Each gonad is enclosed in a special chamber or perigonadial coelom (ovisac, and testis-sac), closed off from the other coelomic spaces, but provided with a coelomoduct leading to the exterior (Text-fig. 80).

The two short ducts from the ovarian sacs come together ventrally to open by the median pore in the adult, except in certain Glossiphoniidae where they may open close together but still separately (Protoclepsid; Livanow, 1902). They open into the sacs by ciliated coelomostomes. The ciliated coelomoducts (vasa efferentia) from the testis-sacs pass forwards and join to a common longitudinal duct (vas deferens) on each side. These two sperm-ducts unite to open ventrally by the median male pore.¹

The aberrant genus *Acanthobdella*, which in so many respects approaches the *Oligochaeta* in structure, alone departs from this plan (Livanow, 1906). The female apparatus conforms to the usual type; but, instead of small segmental testis-sacs, there are two large testis-sacs extending from the tenth to the eighteenth segment, which are still in communication with the

¹ Bürger has shown in his studies on the development of *Nephele* (= *Herpobdella*) in 1891, and of *Hirudo* and *Aulostoma* (= *Haemopsis*) in 1894, that the compound sperm-ducts of leeches are formed by the union of successive outgrowths from segmental rudiments. Each rudiment appears as a thickening of the wall of the coelomic cavity of its segment, and gives rise to a testis, an enclosing testis-sac, and a coelomoduct which grows inwards and fuses on each side of the body with that of the next segment. The foremost rudiments develop no testes but coelomoducts which open into the two horns of a bifurcating ingrowth of the mid-ventral epidermis. A similar process of fusion of two consecutive segmental coelomoducts gives rise to branching sperm-ducts in some *Oligochaeta* (see Text-fig. 80). But in the *Lumbricidae* the compound ducts pass backwards to the male pores instead of forwards as in leeches.

The ovisacs and oviducts develop in much the same way in the female segment. But here the ovary appears as a thickening of the splanchnic peritoneum, and projects into a portion of the coelomic cavity which only later becomes closed off as an ovisac. An outgrowth from each sac joins a median ventral ingrowth of the epidermis. Bürger later, 1902, modified his description, maintaining that there are no median ingrowths and that the ducts are completely mesodermal, an unlikely interpretation which cannot be accepted without better evidence. These details require re-examination.

general coelom in the tenth segment. The coelomoducts are represented by a pair of large funnels and short ducts opening by a median ventral pore on the eleventh segment.

The main points in the development of the nephridia of the Hirudinea were already known in 1894 through the work of Bürger on *Hirudo*, *Haemopsis*, and *Herpobdella* (1891, 1894). Except for the end-bladder, derived later from an ectodermal ingrowth, the whole metanephridium including funnel and canal is developed from a large nephridioblast (Trichterzelle) first identified by Bürger at a stage when segmental coelomic cavities are just appearing in the mesoblastic somites. He figures it in the thickness of the septum between consecutive cavities, separated from the cavity in front by a layer of coelomic epithelium. This nephridioblast buds off a chain of cells behind which, becoming bored through by an intracellular lumen, gives rise to the nephridial canal. The large residual cell in front divides to form the ciliated funnel cells which break through the coelomic epithelium to open into the coelom.¹

¹ Later (1902) Bürger described the development of the nephridioblast more in detail in *Glossiphonia*. According to him the nephridioblast divides into a funnel cell ('Trichterzelle') and a canal cell ('Nephroblast'). Both these cells divide, and from the former arise the three ciliated funnel cells of the adult, while from the latter develops the remainder of the nephridial canal.

The development of the nephridia of *Glossiphonia* has again been studied by Bychowsky (1921), who confirms the conclusion that the whole of the metanephridium arises from a single nephridioblast, except the terminal bladder. A pair of such nephridioblasts are found in segments 7, 8, 9, and 12-22. They are absent in segments 10 and 11 bearing the genital pores. Each nephridioblast divides into an anterior funnel cell ('Trichterzelle') and a posterior canal cell ('Nephroblast'). The former moves inwards towards the coelomic cavity and by division gives rise to funnel, capsule, and a portion of the canal; the latter moves outwards and yields the rest of the coiled canal.

Moreover, Bychowsky goes carefully into the question of the early position of the nephridioblasts. In his earliest stages they are found separately embedded in the general unsegmented 'mesoblast'. Later on, when this layer becomes distinguishable into an inner coelomesoblast and an outer thin ectomesoblast below the ectoderm, the nephridioblast has

The difficult question of the first origin of the nephridioblasts in leeches has not yet been definitely answered. On this point the early observations of Whitman who derived them from ectodermal teloblastic cell-rows, and of Bergh and Nusbaum who derived them from 'mesoblast' are incomplete and unconvincing. Probably they are derived very early from independent ectomesoblastic and certainly not coelomesoblastic cells.

One important point may, however, be now considered as established; it is that the funnel and complete canal are developed from the nephridioblast, and further that the nephridioblast is at first intersegmental in position.¹ From the account given above it will be seen that the excretory organs of the Hirudinea are true metanephridia strictly comparable to those of the Oligochaeta. Though they have their own peculiarities and specializations they resemble the Oligochaete metanephridium in all essentials of structure, function, and development. The genital ducts, on the other hand, are of quite different origin, the oviducal and spermiducal funnels arising as outgrowths from the ovisacs and sperm-sacs like coelomoducts. Thus, the general interpretation of the excretory and genital ducts offered by me in 1895 seems to hold good.

General Summary for Annelida.

The Phylum Annelida is the most important group of the moved outwards. By the time the coelomesoblast becomes segmented and the coelomic cavities appear the nephridioblast becomes lodged between two consecutive somites and the ectoderm. It is clear that at this early stage the nephridioblast is retroperitoneal and intersegmental in position, just as it is at a corresponding stage in the Oligochaete (p. 271). To quote Bychowsky's words: 'Die primäre Lage des Nephridioblasten oder der "Trichterzelle" ist unter dem Dissepimente, zwischen zwei Somiten; später befinden sie sich an der Basis des Dissepimentes, an der Vorderwand desselben' . . . 'die Nephridioblasten an das Ektoderm anstossen' (pp. 102-3).

¹ For the suggestion sometimes made (by Meisenheimer (1909) and A. Meyer (1926)) that the segmental excretory organ in leeches is a mixonephridium there is no good evidence whatever. Indeed, the coelomoducts are present fulfilling their original genital function as gonoducts, and having no connexion with the metanephridia.

Invertebrata for the proper understanding of the morphology of nephridia and coelomoducts, and since the condition of these organs in the various Classes are very varied and somewhat complicated it will be useful for the guidance of the reader to write a short summary of the chief facts and conclusions dealt with in the review given above, leaving out unessential detail. More especially is this necessary as since 1895 many new facts have been discovered which on the whole strongly support the general conclusions reached in my previous paper (Goodrich, 1895).

The Annelida are metamerically segmented Coelomata; and it may be assumed, in accordance with the Gonocoele Theory (p. 123), that their segmental coelomic chambers correspond to the similar genital sacs of the lower Triploblastica (Platyhelminthia, Nemertina). We may also assume that originally each true segment with one pair of somites was provided with one pair of excretory nephridia, and one pair of genital coelomoducts. In the rare cases where many pairs of these organs occur in one segment (Polychaeta, p. 194; Oligochaeta, p. 255; Echiuroidea), this is due no doubt to secondary multiplication.

Except where they take on other functions (for instance in cilio-phagocytal organs, p. 200) there is a marked tendency for the coelomoducts to become reduced (or, as in the formation of nephromixia, to remain only as the open coelomic funnel of the nephridium) or to disappear in anterior and posterior sterile segments, and to be fully developed only in fertile segments. The nephridia likewise may disappear in those segments which have lost the excretory function.

The nephridium is fundamentally retroperitoneal and intersegmental. It is intersegmental, because it is developed from a special cell, nephridioblast, which takes up a position between two consecutive coelomesoblastic somites (p. 271). By division this nephridioblast gives rise to a chain of cells, which becomes hollowed out to form the canal opening to the exterior on the posterior segment, while its anterior end projects through the transverse intersegmental septum into the coelomic cavity of the segment in front. Here the anterior extremity may either remain blind and become provided with flame-cell or solenocyte

(protonephridium, p. 117), or acquire an open nephridiostome (metanephridium, p. 117), or, again, have a coelomostome grafted on to it (mixonephridium, p. 119). The nephridium is retroperitoneal because the pre-septal canal (and nephridiostome) and the post-septal canal retain the covering of coelomic epithelium when they bulge into the coelom.

The coelomoduct, being merely an outgrowth (generally funnel-shaped and ciliated) of the lining epithelium of the coelomesoblastic somite, is also covered by coelomic epithelium in so far as it bulges into the coelom. These paired coelomoducts represent the original gonoducts of Triploblastica in general, and persist as such in the fertile segments of Annelida opening independently to the exterior by genital pores, except when reduced or combined with nephridia to form nephromixia.

The Class Polychaeta may be divided into three groups: Group A, provided in the adult trunk segments with internally closed protonephridia, and Group B, provided in the adult trunk segments with open nephridia. In both these groups the nephridium may combine with the coelomoduct to form a nephromixium. Group C has separate complete metanephridia and coelomoducts, but not fully formed nephromixia.

Group A includes the Families Phyllodocidae, Tomopteridae, Nephthyidae, Glyceridae. Their protonephridia are provided with solenocytes varying in detail and in a manner characteristic of each Family. Typically the coelomoduct opens no longer directly to the exterior, but in the fertile segments comes at maturity to open into the protonephridial canal. Such protonephromixia (p. 119) act both as excretory and genital ducts. The solenocyte-bearing inner end may be lost (Tomopteridae, p. 159). In most, but not in all, Glyceridae and in the Nephthyidae the coelomoduct is reduced and specialized to a cilio-phagocytal organ (p. 200) no longer opening to the exterior, and the genital products escape by dehiscence (p. 201).

In Group B, including the remainder of the Polychaeta, the nephridia in the adult trunk segments are open to the coelom. They open either by a nephridiostome (p. 117); or

with the help of a coelomostome grafted on to the internal extremity.

According to the structure of the nephromixia this Group B may be subdivided into Sections.

Section 1 includes families in which the nephridia are clearly metanephridia with open nephridiostomes, but at sexual maturity become large-funnelled metanephromixia acting as gonoducts in the fertile segments. The Syllidae show this modification most clearly. In *Odontosyllis enopla* the true nephridiostome remains distinguishable as a part of the large compound funnel; but in many Syllids it is more or less completely reduced, and the nephromixium comes to resemble the mixonephridium characteristic of the next Section. Within the Family Hesionidae almost every stage can be found between such a genus as *Irma* with mixonephridium-like organ and *Hesione* in which the nephridiostome is fully persistent although connected with the large coelomostome, and the latter is reduced to a cilio-phagocytal organ without external opening.

This condition seems to lead to that found in the Family Nereidae, where (so far as at present known) the coelomoduct always loses its genital function and remains only as a cilio-phagocytal organ having no connexion whatever with the well-developed metanephridium.

In the various Families of Sections 1 and 2 the nephridiostome has a characteristic structure, and in the Nereidae it is remarkable for the presence of marginal ciliated cytoplasmic processes.

In Section 2, distinguished by the possession of mixonephridia only (p. 119), should apparently be placed three important Families of 'Errantia', the Eunicidae, Amphinomidae, and Aphroditidae.

It is scarcely possible, nor is it necessary in the present state of knowledge, to draw a hard line between Sections 1 and 2; but, if the alleged presence of metanephridia in the anterior sterile segments and large-funnelled mixonephridia in the fertile segments of the Disomid *Poecilochaetus* is correctly described (p. 186), the whole of the Spiomorpha (Families Spionidae, Ariciidae, Megalonidae, Disomidae, Paraonidae, Chaetopteridae) should probably be included in Section 1.

Certain small incompletely known Families, such as the Chrysopetalidae, Pisionidae, Typhloscolecidae, Sphaerodoridae, and Ichthyotomidae, possibly also belong to it.

The remainder of the 'Sedentaria' make up Section 2. Here all the segmental organs (with a few possible exceptions, p. 193) of the adult segments, whether fertile or sterile, are of the typical mixonephridial type. This Section includes the Arenicolidae, Maldanidae, and Oweniidae (p. 189); the Cirratulidae, Opheliidae, Chlorhaemidae, and Sternaspidae. The make-up of the segmental organs of the very specialized *Sternaspis* is still unknown (p. 188).

This Section 2 also includes the Terebellomorpha (Amphictaenidae, Amphoretidae, Terebellidae), and the Serpulimorpha (Sabellariidae, Sabellidae, Serpulidae). In these specialized tubicolous worms the mixonephridia are remarkable for their divergence in structure according to the predominance of the excretory function or the genital (pp. 192-3).

Whatever may have been the phylogenetic history of the mixonephridia in the various Families of Section 2, whether they were derived from proto- or from metanephridia, the fusion of coelomostome with nephridial canal is complete in the full-grown organ, and forms a simple wide-mouthed tube.

Group C includes the single Family Capitellidae in which the coelomoducts retain their original function as gonoducts with gonopores, and remain independent of the metanephridia except that the lip of the coelomostome may come into secondary connexion with that of the nephridiostome. In the species *Notomastus* (*Clistomastus*) *lineatus* the coelomoducts are degenerate, fail to acquire an external pore, and the genital products escape by dehiscence.

Closely related to the Polychaeta are the highly specialized Classes Echiurida and Myzostomida (p. 230 and p. 229). But our knowledge of their excretory organs and genital ducts is still too incomplete to enable us to say more than that they are probably mixonephridia, very specialized in the Echiurida. They help but little in the elucidation of the morphology of these organs in the Annelida in general.

Class Archiannelida.—This Class, including a variety of forms of doubtful affinity, presents a great variety of structure in its nephridia and gonoducts, comprising protonephridia, metanephridia, and probably nephromixia. Of the four Divisions into which the Class has here been provisionally classified (p. 214), Division 4, typified by *Dinophilus*, has segmental protonephridia provided with end-cells of a flame-cell or solenocyte-like nature (p. 215). The single pair of gonoducts (at all events in the male) with ciliated funnels opening into a gonadial sac representing the coelom are doubtless coelomoducts only (p. 219). This free-swimming genus is probably not so much truly primitive as neotenic.

The other three Divisions have metanephridia. Division 1, represented by *Polygordius*, appears to have lost the coelomoducts, the genital products being shed by dehiscence (p. 223). In Division 2, including the Family *Nerillidae*, and Division 3, the Families *Saccocirridae* and *Protodrilidae*, are found gonoducts provided with coelomoduct-like funnels. In the female *Nerilla* only one pair remains; while in the male three pairs, derived from the three fertile segments, join to open by a common ventral gonopore. These three segments are specialized, and only one of them seems to produce functional normal spermatozoa (p. 221). In the *Protodrilidae* some species have metanephridia with a long and twisted canal (so-called 'meganephridia'), and other species have open nephridia with short straight canal (so-called 'brachynephridia'). The latter are possibly nephromixia. No oviducts are present since the ova escape by dehiscence; but sperm-ducts occur in the male in a varying number of segments which are without separate nephridia.

In the case of the 'brachynephridial' species there can be little doubt that the gonoducts are nephromixia, but in the others they may be merely coelomoducts (p. 222). The same doubt exists as to the gonoducts of the *Saccocirridae*. Those of the male have large apparently coelomoduct funnels, and are remarkable for their segmental paired intromittent organs (Text-fig. 60).

Class Oligochaeta.—Except for secondary modifica-

tions the general structure and occurrence of both nephridia and genital ducts are remarkably uniform. The nephridia are all of the metanephridial type, typical coelomoducts serve as gonoducts, and there are no nephromixia the excretory and genital ducts retaining their original independence. The nephridiostome, relatively small and simple and with an internal 'flame' of cilia in the lower forms (Text-fig. 66), becomes enlarged and acquires an upper lip with a marginal row of ciliated cells surrounding a central cell in the higher Families (Text-fig. 65). The canal becomes much lengthened and diversified, but almost always retains its structure as a string of cells perforated by an intracellular lumen. From the initial pair of metanephridia present in each segment throughout the trunk great complications may arise especially in the higher forms. The lumen may branch inside the cells and the canal itself may branch. By subdivision each metanephridium may give rise to many separate nephridia, some with and some without funnels, which become differentiated in structure and function and acquire separate openings to the exterior or even into various regions of the alimentary canal. Thus become established exonephric and enteronephric systems (pp. 224 and 254). There is good evidence that, however complex these systems may be, they are always due to the subdivision or budding of the original pair of metanephridia, or of its early embryonic rudiment (p. 273). The name 'meganephridia' is often applied to the original pair, and 'micronephridia' to their smaller derivatives (p. 242).

This unsatisfactory subdivision, based on mere size, has now been replaced by calling the original paired nephridia 'holonephridia' and those resulting from their multiplication by subdivision 'meronephridia'.

The Oligochaeta are hermaphrodite. Their gonads and corresponding coelomoducts are restricted to a few segments of the mid-trunk (never more than four segments with testes, and two following segments with ovaries). Their number and segmental disposition is characteristic of the various Families. There is no relation established between gonoducts and nephridia, but the latter are often absent in the genital segments of the smaller forms. Apart from the development of copulatory

organs from the ectoderm near the male gonopores, of the junction to a common duct on each side of two consecutive pairs of coelomoducts from the male segments, and the rare meeting of the genital pores to a medio-ventral opening, the genital ducts depart little from the primitive plan. No group of Annelids affords better evidence of the original disposition of nephridia and coelomoducts in two independent segmental series.

This last generalization applies equally to the Class Hirudinea, so closely related to the Oligochaeta. Leaving aside the aberrant *Acanthobdella*, in some respects intermediate, and combining primitive with specialized characters (pp. 288 and 289), most of the features distinguishing the metanephridia and coelomoducts of the Hirudinea from those of the Oligochaeta are related to the secondary invasion of the coelomic cavities by mesoblastic tissue, reducing them to narrow channels and small chambers into which open the nephridiostomes, and gonadial chambers enclosing both gonads and coelomostomes. The much coiled nephridial canal is mostly embedded in the mesenchymatous tissue, and is remarkable for the absence of cilia, the branching of the intracellular lumen, and especially for its enlargement immediately next to the ciliated nephrostomial cells into a capsule lined by flattened epithelium and filled with phagocytes. The cavity of this capsule, as a rule, ceases to communicate with the lumen of the following canal (p. 282); but there is no justification for considering the whole excretory organ as a nephromixium.

In the Ichthyobdellidae the canal may branch and form a network joining together the nephridia of the same and of neighbouring segments. A ciliated ectodermal bladder is particularly well developed in Hirudinidae, in which Family the nephridiostome is complex and subdivided.

The leeches are hermaphrodite, having a pair of ovisacs followed behind by a segmental series of paired testis-sacs. The first pair of coelomoducts (oviducts) join to a median ventral gonopore, and the remaining pairs (sperm-funnels) turn forward and join on either side to longitudinal sperm-ducts which unite to open by a median ventral pore anterior to the female pore.

Ectodermal invaginations at these pores contribute copulatory organs.

In spite of their specializations the Hirudinea conform to the same fundamental plan of two independent segmental series, one of excretory metanephridia and the other of genital coelomoducts, found in the Oligochaeta.

This plan may be derived from a yet more primitive one in which the excretory organs were protonephridia, as is still seen in Group A of the Polychaeta and some of the Archiannelida. The modification of these into metanephridia by the opening of the end-cell to form a nephridiostome has probably occurred independently in Polychaeta, Archiannelida, and 'Clitellata' (Oligochaeta and Hirudinea) (p. 296). It has been shown, both in Polychaeta and Oligochaeta, that the metanephridia pass through a protonephridial stage in development (Text-figs. 74, 76).

These general conclusions are borne out by what we know of the provisional larval nephridia, and of the early development of the nephridia in Annelids. There is good evidence, particularly in *Polygordius* (Text-fig. 62), that the so-called 'head-kidneys' of trochophore larvae of Polychaeta (Text-fig. 55), Archiannelida, and Echiuroida (Text-fig. 64), and the similar organs in embryonic Oligochaeta are merely the first pair of the segmental series of nephridia, specialized in accordance with the general tendency seen throughout Annelids for the more anterior excretory organs to develop and come into function before the more posterior ones which succeed them. Such early larval organs are always protonephridial, and are generally provided with well-defined solenocytes.

Our knowledge of the embryonic development of annelidan nephridia is still very incomplete; but, especially from the study of Oligochaeta and Hirudinea (Text-fig. 76), it is generally held that each whole nephridium (including nephridiostome, but excluding ectodermal bladder when present) is derived from a single mother-cell, the nephridioblast. Further, it must be concluded, in spite of contradictory statements, that the nephridioblast comes not from the coelomesoblastic somite but from a more superficial source, and may be described as of ectodermal or ectomesodermal origin. It passes inwards, and,

either before or after division, reaches a position in the coelomic epithelium forming the posterior wall of a somite (= anterior wall of a septum) where it gives rise by repeated division to the nephridial rudiment, usually in the form of a string of cells. Such nephridioblasts have also been found in Polychaeta.

Concerning the first appearance of the nephridioblast there has been much difference of opinion as to whether they should be considered as mesodermal or ectodermal. In the Annelida, where the coelomesoderm derived in early cleavage from cell 4*d* is distinguishable from the mesenchyme (ectomesoderm or 'larval mesoblast'), it is now clear that the nephridioblasts are of superficial origin, and in those cases where the first appearance of the larval protonephridia has been traced, such as those of *Polygordius* (Text-fig. 63) and various Polychaete trochophores (Text-fig. 53), they are of ectodermal or ectomesodermal origin.

On the other hand, the coelomoducts, whether they become independent gonoducts or combine with nephridia to form nephromixia, always develop as outgrowths from the coelomesoblastic somites.

Thus embryology confirms and strengthens the conclusions of comparative anatomy.

Phylum Ectoprocta.

The Ectoprocta have an extensive coelom, but appear to possess no nephridia: Cori (1893) gave a good description of two coelomostomes in *Cristatella* which open by large ciliated funnels leading by ciliated ducts to a common gonopore to the exterior.

Phylum Endoprocta.

Already in 1895 (Goodrich, 1895, p. 488) we had concluded that the excretory and genital ducts of the Endoprocta conform to the same general plan as that of the Platyhelminths. Since then nothing has been found to alter this conclusion. As shown by the earlier observers (Hatschek, Harmer, Ehlers, and others) there is a pair of short unbranched protonephridia opening by a median pore. Each canal consists of a few cells with a narrow intracellular lumen ending blindly in a single flame-cell (Schulz, 1901; Stiasny, 1905).

The coelom is represented by a pair of gonadial sacs from which two coelomoducts pass outwards, meet, and open by a common pore. The median muscular duct leading to it is probably formed by an invagination of the epidermis near the anus. Anus, genital pore, and excretory pore may open into a common cloaca (Urnatella).

In addition, Nickerson (1910) and Assheton (1912) have described some paired groups of apparently excretory cells with ducts to the exterior in *Loxosoma*, which possibly represent other nephridia but require further study.

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